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MARINE CARRION AND SCAVENGERS

JOSEPH C. BRITTON¹ & BRIAN MORTON²

¹*Department of Biology, Texas Christian University, Fort Worth, TX 76129, USA*

²*The Swire Marine Laboratory, The University of Hong Kong, Hong Kong*

Abstract New definitions of marine carrion and scavengers are provided, the incidence of scavenging as a feeding strategy among marine animals is discussed and important sources of marine carrion are considered. Most major phyla have scavenging members, many of which feed opportunistically.

Carrion is a spatially and temporally infrequent food resource in the sea. In the absence of human interference, we suggest that few marine animals die as a consequence of natural senescence, thereby becoming consistently available as carrion for scavengers. Instead, most death results from predation, so that only scraps are available, ephemerally, to scavengers. Even when a carrion windfall follows a natural mass mortality, e.g. as the result of either a pandemic disease or environmental excesses, i.e. temperature or natural toxins produced during red tides, the resulting available biomass is still an unpredictable addition to the nutrient mosaic of the sea. Carrion, as an infrequent food source has, thus, favoured the evolution of facultative rather than obligate marine scavengers. Notwithstanding, lysianassid amphipods and nassariid gastropods most closely approximate our concept of a marine scavenger. Many species in both groups readily detect, move purposely towards and consume carrion. They also have feeding structures and a digestive system capable of rapid processing and digestion of large amounts of such food. A single meal sustains individuals for long periods. Such scavengers are likely derived from otherwise predatory lineages.

Human interference in marine ecosystems probably has contributed to an overestimation of the importance of marine scavengers as a definable feeding guild. Lysianassid amphipods thus feed on and benefit from fish constrained by fishing nets and nassariid populations increase on polluted, carrion-littered, beaches. Many human activities, e.g. discarded trawler by-catches, channel dredging and oceanic gill netting, influence our perception of the importance of marine scavengers. It is possible, for example, that fluxes in sea bird numbers, especially of gulls, may be related to changing ways in which commercial fisheries dispose of discards and the degree to which landfills are either open or sanitized. Human-engendered carrion in the sea is now a significant source of food for a large variety of opportunistic scavengers and has promoted new fisheries, e.g. those for buccinid whelks and portunid crabs.

Pollution promotes greater levels of available carrion both directly and indirectly. Lethal and sub-lethal effects of pollutants kill or weaken organisms, thereby making them susceptible to predators and/or scavengers. Indirectly, eutrophication fosters excessive plankton enrichment, e.g. red tides, which, in turn, can lead to marine mass mortalities; alternately, human-induced diseases bring about episodic deaths of large marine mammals. The present success of marine scavengers can be attributed to human interference in the sea.

Introduction

That life is as much about death as it is about life is self-evident and, yet, although we know much about the living, little is known about the dead. It is, we suppose, only human nature

to focus attention on the living in order to interpret life's processes and interactions. Palaeontologists exhume skeletal remains to interpret phylogeny and prehistoric ecology but, until recently, few pondered the death history of the corpse, preferring the life-history of the pre-mortem being. Since its introduction (Efremov 1940), the subject of taphonomy, i.e. how physical, chemical and biological processes alter post-mortem remains, has grown steadily. It includes the subjects of biostratinomy, i.e. the sedimentation history of organic remains, and diagenetic fossilization, i.e. their alteration after final burial (Lawrence 1968, Seilacher 1973). The pioneering studies of the German scientists Schäfer, Müller and Seilacher on the processes of life, death and burial in the sea gave substance to the science of marine actuopalaeontology which has subsequently been married into the field of interpretive and experimental taphonomy.

In meticulous, if stomach-churning, observations on the sequence of decay by a variety of marine organisms, Schäfer (1972) showed how corpses of either floating or stranded cetaceans, phocids, birds, fishes and invertebrates decayed, not usually in an orderly fashion, as the perfect remains of Museum galleries would have us believe, but subject to the vagaries of the environment to produce disjointed and often dispersed skeletal fragments. Allison (1990) has shown that the rate of decay of soft tissues is controlled by several factors such as: the supply of oxygen (and other electron donors), environmental factors such as temperature, pH and sediment geochemistry, the nature of the tissue's organic carbon and the composition of the microbial community that attacks it. Taphonomic processes in deep-water environments differ markedly from those in shallow waters (Allison et al. 1991) but, in both areas where aerobic conditions prevail, scavengers usually have a rôle in tissue destruction (Allison 1988). It is well known that terrestrial scavengers disarticulate skeletons. In southern Africa, Gyps vultures strip a carcass of soft tissue, leaving the remains to Bearded vultures which proceed with an ordered disarticulation of the skeleton: limbs, ribs, vertebrae and skull (Brown & Plug 1990). Schäfer only rarely mentioned the rôle of scavengers in the marine processes of decay, although in describing the deterioration of a stranded seal, he noted that (p. 36) "This record does not do justice to the rôle of maggots during the disintegration of the corpse". From large to small, Long (1992) notes that "Nassariid gastropods affect fish taphonomy through skeletal disarticulation, exposure of skeletal elements to pre-depositional erosion, prevention of whole-body transport and disarticulation through differential dispersion of skeletal elements". Fossils of soft-bodied medusae and worms are formed only because of either immediate burial or, in some habitats, the rapid development of microbial veils that protect them from scavengers (Gall 1990).

We have developed an interest in marine carrion and scavengers through a series of recent studies of nassariid gastropods (Morton 1990, Britton & Morton 1992, 1993a, b, Morton & Britton 1991, 1993, Liu & Morton 1994). Although we make no pretence at being anything more than newcomers to this field, we have become acutely aware of the absence of a review discussing the significance of carrion in the sea and the importance of marine scavengers in processing it. Recently, we examined the prevalence of scavenging among marine invertebrates (Britton & Morton 1993a) and concluded that all such animals are facultative scavengers, pursuing another, typically predatory, life-style when carrion is either unavailable or limited. The completion of that review stimulated our interest in the food of scavengers, i.e. carrion, and, again, we seem to have entered an area of little synthesis. This review, therefore, attempts to link the two subjects: carrion and scavengers, and the significance of both in the marine environment.

Do marine animals die naturally, i.e. through senescence? It seems to us, as it has to others (Schäfer 1972), that death in the marine environment as a natural consequence of

aging is unlikely. Rather, unpredictable episodes of illness, disease, parasitism and, probably most significantly, predation takes its toll of the defenceless, enfeebled and infirm to produce a corpse that becomes at least partially available as carrion. The elephant graveyard of fable has yet to be discovered and Mammoth 'graveyards' in Siberia are actually the accumulation of bones and tusks deposited in the bends of rivers (Delort 1990). As far as we are aware, humans are the only species to bury their dead collectively in either mass graves or cemeteries where carrion could be a constant source of nutrition to those other forms of life which consume it. This view must be tempered by the reality that the kills of large terrestrial predators eventually become carrion for scavengers to exploit and that this has led to the evolution of specialist obligate scavengers, most notably vultures (Houston 1986, Coleman & Fraser 1987, Rabenold 1987, Wallace & Temple 1987) and carrion flies (Lord & Burger 1984, Goddard & Lago 1985, Beaver 1986a, b, Pitkin 1986, So & Dudgeon 1990, Ives 1991). In the vastness of the sea, is such carrion so plentiful that groups or lineages of animals have evolved which exploit it obligatorily? We doubt this.

In this review, we analyze the literature from two aspects, i.e. the identity of possible obligate scavengers and the frequency of occurrence of carrion in various components of the marine environment. Although specific scavengers may selectively favour certain types of carrion, apparently, it is of little importance to them as to how a favoured food came to be deceased. Thus, a piece of fish either delivered by line, trap, or other man-made device or discarded as by-catch from a trawl is usually as acceptable to scavengers of fish tissue as any carcass produced and delivered by natural means. Most of what we know about marine scavengers has been learned by attracting them to a suitable carrion bait, but baiting attracts a considerable variety of animals, not all of which employ scavenging as their primary means of obtaining food. These facultative scavengers, whose taste for carrion ranges from occasional to frequent, complicates our survey. Yet, they cannot be ignored, for, as we will demonstrate, there is evidence that, due to massive human intervention in marine ecosystems, scavenging in general and facultative scavenging in particular seems to be increasing significantly. We will show how human activities are promoting artificially the success of certain marine animals which, today, we perceive to be scavengers, but their true faces are hidden behind a mask of trash fish, pollution-engendered death or both. We begin, however, by providing our definitions for "carrion" and "scavengers".

Definitions

Marine carrion

A recent dictionary defines carrion as "dead putrefying flesh" (Lincoln & Boxshall 1987). This definition (but without, necessarily, "putrefaction") may be satisfactory for some terrestrial ecosystems, but it is not entirely suitable for the marine environment. It is perhaps easier to define marine carrion by first specifying what it is not. It is not restricted to organic remains of marine origin. Many terrestrially affiliated species, e.g. wading and other birds, some reptiles and insects, and a variety of mammals, may contribute to marine carrion through death and transport to the sea and its shores. Neither is it dead leaf and other plant structures either grazed or shredded by such animals as mangrove crabs (Sesarinae) (Robertson 1986, Camilleri 1989, Lee 1989a, b, Emmerson & McGwynne 1992). It is

neither protistan nor bacterial cells which, either dead or alive, are small enough to be captured by either a mesh of filaments or an array of tentacles and consumed whole. Carrion is, also, not the skeleton of a metazoan carcass. Endo- and exoskeletal elements may be crushed and consumed but, except for marrow, provide little energetic sustenance to the consumer. Bioavailable minerals, however, may be important for a consumer's own skeletal development. Marine scavengers feeding on skeletally bonded carrion frequently cleanse skeletal elements of all adhering soft tissue, leaving behind the solid carbonate, phosphate or siliceous framework. In the deep sea, representatives of the limpet families Cocculinellidae and Osteopeltidae colonize whale bones and, in the case of the former, fish bones (Marshall 1983). Representatives of other families occur on other pelagically-derived substrata, including squid and octopus beaks (Hickman 1983). All are reported to derive nutrition from substratum-decaying microbes (Marshall 1987). It seems also possible that through radula-scraping they obtain additional nutrient and/or minerals directly from the skeleton upon which they reside.

Carrion often provides those marine organisms capable of accessing it with a unique, nutrient-rich, source of sustenance. Broadly defined, marine carrion includes recently deceased, but not decaying, ingestible and digestible metazoan tissue. It may also include ingestible and digestible products of that tissue such as mucus and/or disintegrating cellular components. In this context, carrion can be envisioned as extending across a graded scale, ranging from the largest conceivable recently deceased metazoan, i.e. a Blue whale, to the smallest, i.e. units of metazoan tissue (Table 1). The scale of carrion is important in several respects. Megacarrion, such as a beached whale, for example, might attract a variety of marine and terrestrial scavengers. With time, it deteriorates to an advanced stage of saprophytic disintegration. Eventually, the putrefying flesh, while possibly attracting some new scavengers, e.g. certain amphipods, polychaetes (Oug 1980) and dipterans (Lord & Burger 1984), becomes unavailable to others. Vultures, for example, will eat fresh but not rotten meat (Houston 1986). Some nassariid gastropods may also find putrefying tissue unpalatable, e.g. *Bullia* sp. prefer freshly-stranded *Physalia* to those which have been lying on the beach for some time (Brown 1982). *Nassarius festivus* from Hong Kong is attracted to recent carrion, but is unresponsive to decomposing bivalve and fish tissue (Britton & Morton, unpubl. obs.). Conversely, *Bullia* sp. also prefer dead, slightly decayed, tunicates (*Pyura*) to newly deceased individuals, the former being the best bait to attract large numbers of these sand-dwelling whelks (Brown 1961, 1982).

At the opposite end of the scale, nanocarrion and ultracarrion are often ingested by either suspension or deposit feeding detritivores, without them distinguishing it from other forms of detritus. Even selective deposit feeding detritivores rarely discriminate as to the origin

Table 1 Scales of carrion.

Scale	Approximate biomass (kg)	Example
Megacarrion	> 100 000	A blue whale
Macrocarrion	100	A seal or dolphin
Mesocarrion	1	A bird or fish
Microcarrion	0.01	A 5-cm clam
Nanocarrion	0.000 1	A planktonic invertebrate larva
Ultracarrion	0.000 000 1	A cell or some components of marine snow

of the detritus they ingest, but focus instead upon either a specific source, e.g. the sediment-water interface boundary (Rhoads 1974), or a range of particle sizes, e.g. as do some irregular echinoids (Goodbody 1960).

As tissue putrefaction and small particle size introduce complications that extend quickly beyond the scope of this review, we will employ a narrower definition of marine carrion: freshly dead metazoan soft tissue at the microcarrion size scale or greater that, because it has not achieved an advanced stage of saprophytic digestion, attracts a variety of consumers which derive significant sustenance from it.

Scavengers

With carrion thus defined, the definition of a scavenger is easier to envisage. Nevertheless, Walker & Bambach (1974) point out that scavenging is not a sharply defined feeding category, but merges with that of deposit feeders. A scavenger does not kill its food, but has the ability to actively consume pieces of a corpse by means of fragmenting appendages, biting or shredding mouthparts, or both. A scavenger must also be able to derive nutritional benefit from such a diet, i.e. such material must be digestible. To differentiate true scavenging behaviour from the fortuitous consumption of animal tissues by non-selective detritivores, we need an additional refinement to our definition. True scavengers must be able to detect carrion, usually by either distance or touch chemoreception, or both, deliberating move toward it, and eventually consume either part or all of it. Such a behavioural sequence, similar to that displayed by a predator seeking prey, leaves open the possibility that there may be both obligate and facultative scavengers. We will eventually come to consider the significance inherent in the possibilities of these two potential types of carrion feeders.

A general survey of marine scavengers

In this survey we emphasize necrophagous animals — those that feed by macrophagous scavenging. Some groups whose members are noted primarily for other feeding habits, e.g. filter-feeding copepods and grazing herbivorous gastropods, will receive scant attention. Conversely, non-scavenging habits are sometimes identified and commented upon, particularly among groups containing a predominance of necrophagous species, primarily as either counterpoints or to comparisons with scavenging members. Similarly, some species with scavenging habits have received greater attention in the literature for a variety of reasons. We will discuss these in greater detail as examples.

Turbellaria

Turbellarian flatworms are mainly carnivorous, e.g. *Stylochus frontalis* feeding on cultivated oysters (Littlewood & Marsbe 1990) and *S. ellipticus* preying on oyster spat and barnacles (Daniel et al. 1983). Many others are either parasitic, notably of echinoderms, i.e. representatives of the Dalyellioida (Jennings 1989, Hertel et al. 1990, Jondelius 1992), or commensal, notably of bivalves (Goggin & Cannon 1989, Murina & Solonchenko 1991).

Some marine species are, however, attracted to dead fish and can be collected by baiting. They may be attracted from several metres, indicating the presence of distance chemosensory receptors (Hyman 1951, Jennings 1957).

Nemertea

Dietary preferences are known for only a few nemerteans. Most are selective carnivores which favour specific prey (McDermott & Roe 1985), i.e. *Lineus viridis* preying on intertidal polychaetes in the Wadden Sea (Nordhausen 1988). Some, however, especially members of the Lineidae, may also be macrophagous scavengers. *Cerebratulus lacteus*, *Gorgonohynchus bermudensis*, *Lineus ruber*, *L. vegetus* and *L. viridis* will feed on either one or more of the following items of dead flesh in aquaria: polychaetes, bivalves, small crustaceans or liver (McDermott & Roe 1985). Lineids employ the proboscis for capture of live prey, but forego its use when scavenging. None of the above species has been observed naturally feeding on carrion, but large numbers of *Parborlasia corrugatus* from shallow Antarctic waters were observed converging and feeding upon recently-killed asteroids, *Acodontaster conspicuus* (Dayton et al. 1974). Non-lineid nemertean scavengers include *Ototyphlonemertes brevis*, an interstitial species reported to congregate and feed upon recently-killed fish (Corrêa 1948).

Nematoda

The sea is likely rich in numerous undescribed nematodes, but dietary preferences are poorly known even for the majority of described, common, species. Many nematodes derive sustenance from "the decomposing bodies of plants and animals" (Barnes 1980), but the scavenging relationship is likely more saprophagous than macrophagous (Hyman 1951). *Diplolaimeloides bruciei*, for example, is a bacterivorous nematode that stimulates decomposition of *Spartina anglica* leaves (Alkemade et al. 1992). The free-living marine nematode *Pontonema vulgare* is a scavenger which lives in sediments of high organic content and accumulates in mass aggregations on the dead bodies of fish, jellyfish, starfish and mussels which have succumbed to acute eutrophication-induced oxygen depletion (Lorenzen et al. 1987, Prein 1988).

Polychaeta

Fauchald & Jumars (1979) point out that the majority of polychaetes are either microphagous suspension feeders or deposit feeding detritivores, e.g. representatives of the Spionidae (Dauer & Ewing 1991). Microphagous scavenging is thus well represented among the Polychaeta. Fauchald & Jumars also recognize 19 families of carnivorous polychaetes. Unfortunately, they fail to list macrophagous scavenging among their otherwise defined polychaete feeding guilds, apparently including this feeding behaviour with carnivory. Many omnivorous polychaetes, e.g. some Nereidae and Nerillidae, ingest animal debris, but not necessarily fresh carrion. Similarly, many families of predominantly carnivorous polychaetes include members which are at least facultative detritivores, with some likely taking carrion. These include the Amphinomidae, Hesionidae, some Lumbrinereidae,

Nereidae, Onuphidae, including *Diopatra* spp. and *Hyalinoecia*, Phyllodocidae (*Eumida* sp.), Polyodontidae, Polyodontidae and Spintheridae. The Hesionidae, including the Danish species *Ophiodromus flexuosus* and *Nereimyra punctata*, possibly utilize chemoreception to help locate carrion (Oug 1980).

The amphinomid *Pherecardia striata* and two other unidentified species feed upon injured and moribund sea stars, especially *Acanthaster planci*, from Pacific reefs off Panama (Glynn 1984a). Because lumbrinerids are difficult to identify, Fauchald & Jumars (1979) were uncertain exactly which species fed on carrion based upon literature reports. They, nevertheless, indicated that macrophagous scavenging is practised by some members of this family. The Nereidae includes species with many different feeding strategies. Omnivores and detritivores are well represented. *Nereis virens* is "an errant carnivore which also feeds on dead animals and algae" (Nicol 1969, p. 238). *Cheilonereis cyclurus* and *Nereis fucata* live as commensals with hermit crabs and steal food from their hosts (MacGinitie & MacGinitie 1968, Goerke 1971a, b). Members of the onuphid genus *Hyalinoecia* are attracted to carrion and hundreds of individuals can aggregate on a single moribund fish (Dayton & Hessler 1972). Another tube-dwelling onuphid, *Diopatra cuprea*, captures live prey, scavenges detritus which attaches to the elevated chimney of its tube and feeds opportunistically upon nearby carrion (Mangum et al. 1968, Myers 1972). Spintherids are apparently either carnivorous or ectoparasitic on sponges, and may ingest sponge carrion (Fauchald & Jumars 1979). Other polychaete families include species with highly variable diets and may rely, at least in part, on either carrion or animal detritus.

Mollusca

The Cephalopoda are mostly predators of living fish, prawns, crabs and even other cephalopods (Boucaud-Camou & Boucher-Rodoni 1983, Sauer & Lipinski 1991), but some deep-sea octopods are attracted to fish bait (Isaacs & Schwartzlose 1975). Among the bivalves, only representatives of the deep water genera *Poromya* and *Cuspidaria* were considered scavengers of planktonic-derived carcasses (Yonge 1928). These, and other members of the "septibranch" Anomalodesmata, are now known to be active predators (Reid & Reid 1974, Morton 1981).

Macrophagous scavenging appears sporadically among several diverse predatory Gastropoda. The muricid *Chicoreus pomum*, which normally drills bivalve shells and feeds on the tissue inside (Radwin & Wells 1968), is also attracted to and feeds upon fresh fish carcasses, but is unresponsive to dead fish which have been in the water for more than a few hours (J. C. B. pers. obs.). *Thais orbita* (= *Dicathais aegrota*), typically a molluscan predator, comes to bait (Phillips 1969) and feeds upon natural carrion (Morton & Britton 1993) on shallow intertidal rock platforms in Western Australia. The olive snail, *Oliva sayana*, normally a predator of small bivalves, crustaceans, polychaetes and other invertebrates, also feeds upon fish carrion (Kohn 1961). Species of the opisthobranch *Pleurobranchus* prey upon ascidians, sponges and other attached invertebrates, but also ingest various kinds of carrion when it is available (Nicol 1969). Weaver & duPont (1970) reported that the volutes *Adelomelon beckii* and *Cymbiola aulica* are sometimes taken by fishermen on baited fish hooks; a review of the diets of members of this family, however, has shown them to be specialized predators of bivalves and, especially, other gastropods (Morton 1986c).

Macrophagous scavenging is a principal feeding habit in three closely related families of the Neogastropoda: the Buccinidae and Melongenidae, but especially the Nassariidae,

which, with several less significant families, constitute the Buccinoidea. The roots of neogastropod scavenging are usually traced to a remote predatory ancestor (Fretter & Graham 1962, Ponder 1973), but scavenging may have been a trophic niche among the gastropods longer than previously perceived. The Buccinoidea are of relatively recent ancestry, with the Buccinidae and Melongenidae derived from the mid-Cretaceous and the Nassariidae from either the late Cretaceous or early Tertiary (Taylor et al. 1980, Hansen 1982). Yet, based on species abundance trends of *Subulites* (of the now extinct Subulitidae) from an Ordovician (Palaeozoic) fossil bed, Stanley (1977) discounted the notion of Cameron (1967) that they were representative of the earliest carnivorous gastropods, suggesting instead that they were microphagous and/or macrophagous scavengers. If true, it places scavenging behaviour near the early antiquity of the gastropods and suggests that necrophagous gastropod scavenging may have arisen independently several times.

An examination of the diets of representatives of the Buccinidae and Melongenidae might cast light on the origin of necrophagous scavenging in the modern Buccinoidea. Large whelks often exhibit catholic diets. *Buccinum undatum*, which is collected commercially in carrion-baited pots (Sainte-Marie 1991), was once considered to be predominantly necrophagous (Dakin 1912). It does scavenge (Himmelman 1988), often moving rapidly toward baited pots (Gros & Santarelli 1986, McQuinn et al. 1988, LaPointe & Sainte-Marie 1992) and permitting the development of a substantial fishery, e.g. off the Atlantic coast of France, but is also a generalized predator. Taylor (1978) identified 35 species of presumed prey belonging to eight animal phyla from *B. undatum* gut contents. Nielsen (1975) describes how *B. undatum* feeds upon living bivalves by wedging the tip of its shell between parted valves, inserting its proboscis in the gap and using the radula to tear out flesh. In the Mediterranean, *B. corneum* feeds mainly upon sabellid and eunicid polychaetes but also eats gastropods (Taylor 1987). Another buccinid, *Cominella eburnea*, scavenges upon Western Australian shores, but it is principally a bivalve predator (Morton & Britton 1991). In New Zealand, *Cominella glandiformis* is reported to commonly scavenge moribund bivalves, especially *Austrovenus stutchburyi* (Walsby 1990). In Puget Sound, Washington, USA, the rocky intertidal buccinid, *Searlesia dira*, feeds on barnacles, limpets and chitons, although other prey and carrion are also taken (Louda 1979). Four species of *Neptunea* feed primarily upon bivalves and polychaetes, secondarily upon carrion, with other prey taxa also represented in their diets (MacIntosh 1980, Shimek 1984). *Babylonia lutosa* from Hong Kong is a scavenger (Morton 1990) but analyses of gut-contents from field-collected individuals suggests that they may primarily predate polychaetes (Taylor 1982, Taylor & Shin 1990).

The Melongenidae also contain opportunistic scavenging representatives, especially those species of *Melongenella* and *Busycon* from the Western Atlantic. Most are primarily bivalve predators (Magalhaes 1948, Paine 1962) that occasionally scavenge. In coastal Cape Cod waters, two species of *Busycon*, i.e. *B. carica* and *B. canaliculatum* feed selectively on different components of the bivalve fauna (Davis 1981). *Melongenella corona* in the northern Gulf of Mexico feeds upon the solitary ascidian *Styela plicata* (Dalby 1989). Similarly, Western Pacific melongenid whelks of the genus *Hemifusus* consume some carrion, but are also principally bivalve predators (Morton 1985, 1986a, b, 1987).

The Nassariidae contain some of the best known necrophagous molluscs, but the diets of several members of this family are decidedly capricious (Taylor 1981, Taylor & Shin 1990). In fact, of the approximately 317 living species of Nassariidae (Cernohorsky 1984), the diets of <10% are known (Britton & Morton 1993a). A few are shallow subtidal species, but most are intertidal. The subtidal South African *Bullia laevissima* feeds on carrion in relatively non-turbulent shallow waters (Brown 1961). Similarly, the subtidal California species

Nassarius mendicus (Britton & Morton 1993b) and the subtidal Hong Kong species *N. siquijorensis* (Liu & Morton 1994) both detect, move purposely toward and consume carrion, but lack the long-range chemoreception ability of their intertidal counterparts. The few shallow subtidal nassariids whose gut contents have been examined, e.g. *Nassarius albescens* and *N. arcularis* from the Red Sea (Taylor & Reid 1984) and *N. siquijorensis* and *N. crematus* from Tolo Channel and Mirs Bay, Hong Kong (Taylor & Shin 1990) usually include numerous polychaete and crustacean fragments, sediment, detritus and various other vertebrate and invertebrate skeletal elements.

Intertidal *Bullia digitalis* and *B. rhodostoma* of South African sandy beaches also feed on carrion, especially cnidarians, which are stranded either within or slightly above the beach wash zone (Brown 1982). Typically, however, the former species actively seeks mussel and other carrion in the surf by swash-riding (Odendaal et al. 1992). *B. digitalis* will also take live prey (Brown 1971, 1982, Brown et al. 1989) and feeds on green algae attached to its shell (da Silva & Brown 1984, Harris et al. 1986). *Nassarius kraussianus*, also from South Africa, can survive at least two months by grazing upon algae in the absence of a preferred diet of carrion (Brown 1982).

Ilyanassa obsoleta, from the temperate Western Atlantic, feeds upon carrion when available but is, primarily, a deposit-feeding omnivorous detritivore (Scheltema 1964), with sediment and macroalgal fragments dominating the gut contents (Curtis & Hurd 1979). The latter authors demonstrated experimentally that *I. obsoleta* is an obligate omnivore, requiring a mixed diet of both plants and animals. Notwithstanding, the attraction of *I. obsoleta* to carrion has been known at least since the work of Dimon (1905). Jenner (1956) surmised that since carrion was relatively scarce, it could not be the main source of energy for such an abundant snail. It has been shown, however, that carrion is more than an incidental requirement since meat is essential for survival, growth and female reproduction in this species (Curtis & Hurd 1979). Recently, Curtis (1985) has shown that: (a) males and females respond differently to carrion; (b) attraction is sometimes predominantly a female response and (c) trematode parasites influenced the responses of both males and females to carrion.

Food preferences of *Nassarius reticulatus* from Gullmar Fjord on the western coast of Sweden (Tallmark 1980) vary with size and age. Younger, smaller, individuals feed mostly upon detritus from fine, unconsolidated, sediments but larger, older, animals prefer carrion, especially moribund cockles. *N. festivus* from Hong Kong and *N. pyrrhus* from Western Australia feed upon freshly moribund bivalves, fish and decapod crustaceans (Morton & Britton 1991, Britton & Morton 1992). It is not known, however, if either of these species have additional dietary preferences. The omnivorous *N. pauperatus* from South Australia feeds on algae and carrion (McKillup & Butler 1979), especially moribund *Katelysia scalarina*, a sandflat bivalve, which is also scavenged by *N. pyrrhus* (Morton & Britton 1991).

The shell shape of several Nassariidae, e.g. *Bullia digitalis*, facilitates their burial within unconsolidated substrata (Trueman & Brown 1989). *Cyclope neritea*, *Hinia reticulata* and *Sphaeronassa variabilis* generally repose within the substratum during the day with only the tips of their siphons exposed (Bedulli 1976). More robust species, such as *Ilyanassa obsoleta*, may also seek shelter by burial, but the accumulation of extensive mats of filamentous algae upon their shells suggests that other sites of repose are also utilized. Most nassariids either emerge from the substratum or otherwise become active when food is placed within the range of detection (Trueman & Brown 1987, Morton & Britton 1991, Britton & Morton 1992, 1993b). An immediate increase in oxygen uptake accompanies this activity (Crisp et al. 1978). Nassariids are acutely sensitive to physical and chemical stimuli,

the latter conveyed either by contact or water. Aspects of chemoreception in nassariids and other scavengers will be considered in a separate section.

Arthropoda

The arthropod digestive tract is designed primarily to process either finely particulate or liquid foods. Mastication, tissue shredding and particle sorting, if occurring at all, does so externally. Accordingly, many arthropods are facultatively and/or actually microphagous gatherers, with feeding structures designed to extract nutrients either from fluids or soft sediments. Arthropods which gather organic detritus floating in water are included among suspension feeders, but those which extract it from sediments are microphagous scavengers.

Not all arthropods selectively ingest fine particles. The extreme adaptability and plasticity of their appendages have liberated arthropods from compulsory microphagous diets. Raptorial arms, chelipeds, fangs, stingers and other structures enable many arthropods to capture and hold large objects. The capturing appendages and/or additional ones near the mouth often reduce large food items to fine particles prior to it entering the digestive tract. If, however, larger food particles such as either shredded vegetation or bits of flesh enter the digestive tract, they are usually well pulverized in an internal gastric mill, gizzard or similar structure of the foregut prior to digestion and assimilation. The specific form and function of food-gathering appendages varies widely throughout the Arthropoda, permitting a diversity of microphagous and macrophagous diets and feeding behaviours (including suspension feeding, suctorial fluid ingestion, herbivory, carnivory, omnivory, detritivory and scavenging). Thus, arthropod feeding strategies are not constrained by mechanical demands of either the digestive tract or feeding process (as, for example, are many gastropod and most bivalve molluscs), but have been free to evolve according to the availability of nutrients in the environment and the adaptability of appendages to deal with them. Like other animals, some arthropods have highly specialized diets. Notwithstanding, many taxa, at a variety of levels from species to order (especially among the Crustacea), have developed a repertoire of feeding strategies which they exercise selectively depending upon the food available (Grahame 1983). These arthropods move easily from microphagous scavenger to macrophagous carnivore, herbivore, omnivore or scavenger. This makes it difficult for us to generalize with respect to arthropod macrophagous scavenging, for it appears opportunistically in many groups.

Merostomes are a good case in point. The Atlantic *Limulus polyphemus*, the Indo-Pacific *Tachypleus tridentatus* and other extant merostomes are well-adapted for microphagous scavenging. Small chelate appendages collect fine detritus from unconsolidated sediments and transfer it to the gnathobases where it is pulverized further before being passed anteriorly to the mouth. Yet, organic detritus is only part of the diet. Horseshoe crabs opportunistically capture and ingest bottom dwelling algae and live prey — mostly benthic worms, molluscs, and other small invertebrates — all of which are subjected to the same particle-reducing process before entering the digestive tract. It is a small step from live prey to macrophagous carrion, which is also processed and ingested when available. It is likely that carrion is detected by chemoreceptors located on spines on the coxal gnathobases of the walking legs, on chelae, chelicerae and other prosomal appendages, and on chilidia spines (Barber & Hayes 1963).

Pycnogonids are not especially noted for necrophagy, but eight Antarctic species representing three families have been caught in carrion-baited traps (Arnaud 1972; Arnaud

& Bamber 1987). Most were taken at depths of between 25–85m, but two species, *Pentanymphe antarcticum* and *Ammonothea glacialis*, were caught at a depth of 320m.

Many small, free-living, non-malacostracans of necessity feed upon microphagous particles. Planktonic species usually do this by either suspension or filter-feeding. Conversely, the primitive cephalocarid, *Hutchinsoniella macracantha*, is a suitable simple model of a benthic, non-selective, microphagous scavenging arthropod (Sanders 1963). The movements of similar pairs of thoracic limbs produce a current of water in which seston is drawn into the medial space between limb pairs. Such material is caught by setae and transferred into a ventral food groove, wherein it passes forward to the mouth. This basic model, though modified, embellished, perfected and frequently made selective by other crustaceans, apparently represents a fundamental feeding method for benthic aquatic arthropods (Manton 1977).

Body size and food resources, however, are not strictly correlated in the Crustacea. Some balanoid barnacles number among the largest non-malacostracans, but feed mostly upon microplankton and seston. In contrast, some benthic ostracods and copepods either capture or feed upon food items half or more their size (Kaestner 1970), as do some freshwater branchiopods (Marshall & Orr 1960). In comparison to the total number of species of Crustacea, the number whose diet and feeding habits have been investigated is small, with many tiny non-malacostracans being especially poorly known. It is clear, however, that some groups of predominantly small-bodied non-malacostracans express the same diversity of feeding habits as are found in larger malacostracans.

Ostracods and copepods are best known as either suspension feeders or microphagous detritivores, but both groups contain members which demonstrate several other feeding behaviours. Predatory myodocopid ostracods, including *Gigantocypris mulleri*, *Conchoecia* sp., *Cypridina castanea* and *C. norvegica*, capture copepods, mysids, euphasiids, chaetognaths, polychaetes and fish fry (Cannon 1933, Hardy 1956, Lochhead 1968, Kaestner 1970). Species of *Cypridina* and *Vargula* are scavengers of planktonic carrion. Benthic carrion-feeding podocopid ostracods include *Paradoxostoma variabilis*, *Macrocypris* sp. (Cannon 1933) and several freshwater species (Kaestner 1970). Several predatory cyclopoid and calanoid copepods will also eat recently-dead carrion; many benthic harpacticoids are microphagous detritivores, and some freshwater Cyclopidae feed upon fish carrion (Fryer 1957). The planktonic cyclopoid copepod, *Oncaea mediterranea*, crawls upon and scavenges the mucous walls of abandoned larvacean houses while other crustaceans, such as the harpacticoid *Microsetella norvegica*, the calanoid *Paracalanus aculeatus* and the ostracod *Conchoecia rotundata*, may supplement their diets with the rich field of nanoplankton that becomes trapped upon the floating mucous houses of larvaceans (Alldredge 1972).

Barnacles are predominantly filter-feeding crustaceans, but *Lepas anatifera*, *Pollicipes polymerus* (Howard & Scott 1959) and *Tetraclita squamosa* (Marshall & Orr 1960) capture and ingest copepods, amphipods, isopods, polychaetes and tiny gastropods and bivalves. Contact with any of these potential food items is passively opportunistic; the characterization of feeding behaviour as either predation or scavenging thus depends upon the condition of the food item when contact is made with the barnacle cirri. Kaestner (1970) has stated that when lepadomorphs, such as species of *Lepas* or *Scalpellum*, are presented with small pieces of meat, their cirri will grasp it and pass it to the mouth.

Microphagous detritivory is widespread throughout the Malacostraca, including the primitive freshwater syncarideans such as *Anaspides tasmaniae* (Cannon & Manton 1929, Williams 1965), the monophyletic *Spelaeogriphus lepidops*, known only from a single South African stream, tanaidaceans, cumaceans, isopods, amphipods and numerous

decapods. Many of these species are also opportunistic macrophagous scavengers.

As with most other major groups of marine arthropods, it is difficult to formulate a generalized decapod diet, for this diverse group exhibits a wide range of feeding habits. In addition to primary feeding behaviours that differ widely among species, many decapods are also facultative necrophagous scavengers, including, but not restricted to various Anomura (especially hermit crabs) and representatives of the Majidae, e.g. *Libinia emarginata* (Aldrich 1974), Cancridae, e.g. *Cancer irroratus* (Caddy 1973), Portunidae, e.g. *Callinectes sapidus* (Williams 1984), *Scylla serrata* (Hill 1978, 1979), Xanthidae, e.g. *Menippe mercenaria* (Powell & Gunter 1968), Ocypodidae (Teerling 1970) and Gecarcinidae (Wolcott 1988).

Many predominantly herbivorous, semi-terrestrial, Anomura are also opportunistic macrophagous scavengers. *Coenobita perlatus* is such an efficient scavenger on Indo-Pacific islands that the low numbers of carrion flies on many of them is attributed to its presence (Alexander 1979, Page & Willason 1982). The Western Atlantic *Coenobita clypeatus* will feed upon virtually any carrion it encounters. De Wilde (1973) provides a vivid account of hundreds of *C. clypeatus* feeding on the carcass of a dead donkey. Even the predominantly herbivorous coconut crab, *Birgus latro*, scavenges for animal protein (Grubb 1971, Alexander 1979). Individuals maintained for prolonged periods in the laboratory are reported to require it (Harms 1932).

Intertidal and shallow subtidal anomurans are also known to scavenge carrion. *Hippa pacifica* feeds upon stranded *Physalia*, ingesting zooids and fishing tentacles with nematocysts (Matthews 1955). Various hermit crabs, especially intertidal representatives of the Diogenidae, are macrophagous carrion scavengers in addition to being microphagous detritivores (Bolt 1961, Roberts 1968). On many beaches, either one or more diogenid crustaceans compete with nassariid scavengers for carrion resources (Britton & Morton 1991, 1993a). Intertidal hermit crabs often feed in cycles correlated with tidal flux. For example, *Calcinus latens* actively forages for either detritus or carrion at low tide but finds shelter under rocks and coral boulders at high tide (Reese 1969). Conversely, *Clibanarius cubensis* is active during high tides, day and night (Hazlett 1966). Other hermit crabs forage primarily at night, e.g. *C. tricolor*, *Calcinus tibicen* and *Pagurus miamensis*. One of us (J. C. B.) was able to attract *C. tricolor* to fresh bivalve and crab baits during morning low tides, but not afternoon high tides (total tidal range < 0.33 m). *Trizopagurus magnificus*, from Pacific Panamanian coral reefs, feeds occasionally on dead and moribund asteroids (Glynn 1984a).

Many semi-terrestrial Brachyura, despite a primary dietary preference, also engage in macrophagous scavenging. Sandy beaches throughout the world are occupied by ocypodid ghost crabs, most of which are predators (Wolcott 1988) that also take carrion. Some, such as the Western Atlantic *Ocypode quadrata*, were once considered exclusively scavengers. In fact, *O. quadrata* is another example of arthropod adaptability and facultative scavenging, preying upon beach macrofauna, i.e. mole crabs and surf clams, for 90% of its diet (Wolcott 1978), but feeding upon a variety of carrion and decaying vegetation, including *Sargassum*, insects, fish, cnidarians, other ghost crabs, turtles and even cetacean and bovine carcasses (Teerling 1970). This species is equally adept at microphagous scavenging (Robertson & Pfeiffer 1982). The Western Pacific species, *Ocypode ceratophthalmus*, has a similarly broad range of feeding behaviours (Jones 1972).

Ghost crabs which share sandy beaches often partition the environment with respect to both vertical shore position and feeding preferences. *O. cordimana*, an east African supratidal species, feeds upon insects, ants, small reptiles and carrion (Burggren & McMahon 1988). A lower shore species, *O. ryderi* (= *O. kuhli*), relies upon macrophagous algae for

long-term sustenance, but also takes either living or recently moribund hippids, congeners and insects. When presented with a choice, *O. ryderi* prefers animal to plant food (Evans et al. 1976). The painted ghost crab, *O. gaudichaudii*, from Costa Rica feeds upon detritus and both living and dead plant and animal tissues (Trott 1988).

The Grapsidae is a large, diverse, family with many semiterrestrial species. Some are herbivorous, e.g. the rocky shore *Grapsus grapsus*; some are detritivores, e.g. the mangrove-dwelling species of *Chiromantes*, which process mangrove leaf litter (Malley 1978, Lee 1989a, b); some are decidedly omnivorous, e.g. *Aratus pisonii*, which feeds upon mangrove leaves and preys upon insects and juvenile conspecifics (Warner 1967, Beever et al. 1979) and some are mainly carnivores, e.g. *Goniopsis cruentata*, which preys upon *Aratus pisonii*, species of *Uca* and other mangrove fauna (Warner 1967). Many grapsids, despite their preferred cuisine are, however, also facultative scavengers. Species especially noted for their diet of carrion include *Geograpsus crinipes* from sandy beaches throughout the Indo-Pacific (Alexander 1979), *G. stormi* from rocky shores in the same region (Gilchrist 1988) and *Sesarma roberti* from coastal forests of the Caribbean basin (von Hagen 1977).

Representatives of the Gecarcinidae are predominantly herbivores, feeding upon leaves, fruit, algae, mosses and other plant products (Wolcott 1988); but all members of the family are also opportunistic scavengers. Even mangrove-dwelling species, e.g. *Cardisoma guanhumi*, which are mainly leaf-litter detritivores, readily take carrion when it is available (Herreid 1963). Higher upon the shore, various species of *Gecarcinus* not only scavenge carrion but, sometimes, feed upon living insects, young reptiles, juvenile conspecifics and other prey (Fimble 1975, Bliss et al. 1978, Wolcott & Wolcott 1984). *G. planatus* from Clipperton Island is particularly notable for its aggressive consumption of any animal protein, either living or dead, which comes within its grasp (Ehrhardt & Niauxsat 1970).

Isopod diets are as varied as those of most other large malacostracan groups. Microphagous scavenging seems to unite the benthic isopod fabric, but several different threads contribute to the weave. Many isopods favour detritivory on either mud or sand, especially within decaying vegetation. Others, such as the gribble *Limnoria*, are highly specialized herbivores of wood. Predators and parasites are common, as are macrophagous carrion scavengers. The Cirolanidae and Idoteidae include many fish predators, e.g. *Nerocila acuminata* (Segal 1987), but also several well-known carrion-feeders. *Natatolana* (= *Cirolana*) *borealis* of north European coasts feeds primarily upon fish and crustacean carrion (Nickell 1989) and is reported to attack both diseased and netted fish (Vader & Romppainen 1986). *Cirolana hartfordi* frequents rock-strewn sandy beaches of North American Pacific shores. It captures and feeds upon living polychaetes and amphipods, but is attracted to carrion, especially fish, detecting it from considerable distances by chemoreceptors (Johnson 1976a, b). Hundreds of individuals often gather at a dead fish and reduce it to bones within a few hours. *Chiridotea coeca*, occupying the sandy beaches of temperate eastern North America, seizes carrion with its gnathopods and bites off pieces with its mandibles (Nicol 1969). *Glyptonotus antarcticus* is a shallow subtidal scavenger of the Southern Ocean (Dearborn 1967). These and numerous other isopods rely upon carrion as a central component of their diets. Still others are opportunistic carrion scavengers. Species of *Ligia* are primarily algal herbivores, but feed readily upon carrion when it is available (personal observations). Species of *Serolis* are mostly detritivores, but will also feed upon decaying meat (Kaestner 1970). Even the predominantly herbivorous *Idotea emarginata* will feed upon carrion when it is available (Naylor 1955).

Along shelf margins, large cirolanid isopods come to baited traps. In the Gulf of Mexico, the largest known isopod, *Bathynomus giganteus*, can be attracted to fish bait at depths of

between 349–733 m off Yucatan (Briones-Fourzán & Lozano-Alvarez 1991), but it also preys upon sessile and slow-moving animals such as tunicates and echinoderms. *B. doderleini* was captured in traps baited with chopped fish at depths of between 250–550 m off Taiwan (Tso & Mok 1991) and Japan (Sekiguchi et al. 1982), but was never taken in traps set in waters shallower than 150 m (Sekiguchi et al. 1982).

Many, if not most, Amphipoda incorporate some form of scavenging in their feeding repertoire, especially microphagous detritivory. However, the amphipod families Lysianassidae and Talitridae include some of the better known macrophagous amphipod scavengers. Chemoreceptor organs on the antennules of both deep-water and shallow-water lysianassid amphipods are used for distance chemoreception; most other amphipod groups lack them (Dahl 1979). Lysianassids also display other morphological adaptations for carrion feeding such as unique mandible modifications and alimentary canals adapted for storage of large quantities of food (Dahl 1979). Large numbers of *Orchomenella nana*, *Tmetonyx cicada*, *Anonyx* sp. and *Scopelocheirus* sp. are attracted to fish carrion on sandy North Sea shores (Kaestner 1970, Vader & Romppainen 1986). *Orchestia gamarella* and *Talitrus saltator* are opportunistic omnivores which scavenge small fish and other carrion washed upon Mediterranean beaches. *Psammonyx nobilis*, an inhabitant of well-sorted, fine, sand on temperate Western Atlantic (New England) beaches, aggregates upon carrion washing ashore (Scott & Croker 1976). Many of these amphipods forage on carrion, flotsam and detritus according to endogenous activity rhythms (Wildish 1970, Bregazzi & Naylor 1972).

Amphipod scavengers, however, are not limited to intertidal sands. Carrion-eating lysianassids play an important rôle as scavengers in Norwegian and Arctic waters. Species of *Anonyx* and *Tmetonyx* damage fish caught in nets and on long-lines while numerous other species are parasites (Vader & Romppainen 1986). From the central North Pacific, free-vehicle baited traps attracted four dominant species of amphipods (Ingram & Hessler 1983).

Scavenging amphipods are also relatively common inhabitants of unconsolidated sediments on continental shelves (Nickell 1989) and deep-sea floors (Hessler 1974, Shulenberger & Hessler 1974, Shulenberger & Barnard 1976). In the Saint Lawrence estuary, baited traps lured five species of lysianassids accounting for between 75.0–99.9% of all the scavengers attracted (Sainte-Marie 1986a). Of these, species of *Anonyx* are apparently better able to compete for large carrion than species of *Orchomenella* (Sainte-Marie 1986b). In a survey of more than 40 species of epibenthic scavenging invertebrates from subtidal continental shelf habitats, all but two were trophic generalists (Nickell 1989). Only the lysianassid amphipod *Scopelocheirus hopei* and the cirrolanid isopod *Natatolana borealis* were found feeding only upon carrion. Scavenging lysianassids are discussed in more detail in subsequent sections of this review.

Caine (1974) records four methods of food acquisition among caprellid amphipods: predation, scavenging either detritus or carrion, scraping sessile epibenthos and filter feeding. Some species seemed to have a restricted feeding repertoire, such as the mostly predatory *Luconacia incerta*. Others have more catholic habits. *Caprella penantis* combines filter-feeding and scraping behaviours; *Paracaprella tenuis* employs all four feeding methods.

Insects, especially representatives of the Diptera, Coleoptera and some Hymenoptera (ants), frequently dominate carrion-consuming scavengers of the upper shore. In a study of sea bird carrion on islands in the Gulf of Maine, the impact of amphipods and decapods was decidedly secondary to that of insect scavengers in the decomposition of carcasses (Lord & Burger 1984). Coleopterans which may resort to feeding on seashore carrion include the Staphylinidae (rove beetles), the Cicindelidae (tiger beetles), the carrion-feeding members of the Nitidulidae (sap beetles) and the Scarabaeidae. Beach-dwelling members of the

dipteran Anthomyiidae (kelpflies), especially species of *Fucilia*, are known to feed upon beached carrion.

Echinodermata

Echinoderm scavengers include members of the Asteroidea, Ophiuroidea, Holothuroidea and a few Echinoidea. Many adult predatory asteroids exhibit a juvenile predilection for scavenging. Prior to adopting the adult diet, juvenile *Linckia laevigata*, *Mediaster aequalis*, *Asterina gibbosa*, *Henricia leviuscula* and *Stichaster australis* have been described as variously discriminating detritivores (Sloan 1980 and references therein), whereas juvenile *Luidia ciliaris* feed upon asteroid and molluscan carrion within a week of metamorphosis (Wilson 1978).

The focus of asteroid scavenging varies considerably. Species of *Asterina* from the Indian Ocean and Australia are microphagous scavengers, feeding upon detritus, surface films, diatoms and bacteria (Crump & Emson 1978, Emson & Crump 1979). Normally predatory *Asteropsis carinifera*, *Choriaster granulatus*, *Linckia guildingi*, *L. laevigata*, *Protoreaster nodosus* and *Patiria pectinifera* from the Central Pacific, *P. miniata*, *Pisaster brevispinus*, *P. giganteus* and *Pycnopodia helianthoides* from the Eastern Pacific, *Oreaster reticulatus*, *Echinaster serpentarius* and *Asterias forbesi* from the Western Atlantic, *Henricia oculata* from the Eastern Atlantic, *Cuenotaster involutus*, *Porania antarctica*, *Diplasterias brucei*, *Lyasterias perrieri* and *Neosmilaster georgianus* from Antarctica and *Patiriella brevispina* and *Coscinasterias calamaria* from Southern Australia have been reported to feed upon carrion (Sloan 1980, Sloan & Campbell 1982, Jangoux & Lawrence 1982; and references therein). The normal prey of these species varies, but includes bivalves, gastropods, polychaetes, barnacles and other echinoderms. Several of these carnivorous asteroids employ chemoreception to detect both prey and carrion (Sloan & Campbell 1982). Meat juices (Romanes 1883), acetylcholine (Anderson 1953), coral extracts (Collins 1974, Ormond et al. 1976) and various proteins and amino acids (Heeb 1973, Valentinčič 1975) stimulate feeding responses in various asteroids. Wobber (1975) comments upon the scavenging behaviour of *Patiria miniata* from Monterey Bay, California. This opportunistic asteroid will aggregate on any available carrion and aggressively jousts for a suitable feeding position.

Despite having the simplest digestive system of the echinoderms, representatives of the Ophiuroidea have a surprisingly diverse inventory of food and feeding behaviours. They include herbivores, carnivores and omnivores obtaining food by deposit feeding, suspension feeding and microphagous and macrophagous scavenging. Many species employ several different feeding behaviours opportunistically. Microphagy occurs widely throughout the class although macrophagous scavenging is probably more common than previously acknowledged. Warner (1982) differentiates between microphagous and macrophagous scavenging ophiuroids in that the former utilize particles small enough to be passed to the mouth by podia, whereas the latter manipulate food particles either by arm or whole body movements. Several ophiuroids, including *Ophiura albida*, *O. texturata*, *Ophiocomina nigra* and *Ophiothrix fragilis*, have been observed feeding on dead fish in aquaria (Nagabhushanam & Colman 1959). *Ophiura lutkeni* grasps carrion in its jaws and applies leverage with its arms to tear flesh from a moribund fish (Austin 1966). Several Antarctic ophiuroids, including *Astrotoma agassizii*, *Amphiophiura brevispina*, *Ophiacantha vivipara*, *Ophionotus victoriae*, *O. hexactis* and *Ophiosparte gigas* were attracted to fish-baited traps in the natural environment (Arnaud 1974). Warner (1982) lists 23 species of necrophagous ophiuroids, although none of these feeds exclusively upon carrion.

Most holothurians are either deposit or suspension feeders but a few, mainly deep-sea Elasipodida, are known to be macrophagous carrion feeders (Massin 1982). Pawson (1976) reported upon a species of *Scotoplanthes* attracted to fish remains. Hessler (1972) obtained elasipods from baited traps and Laubier & Sibuet (1977) captured *Peniagone* sp. in a similar way. The echinoid *Diadema mexicanum* from the Pacific coast of Panama has been observed rasping the tissues of dead crown-of-thorns sea stars, *Acanthaster planci* (Glynn 1984a).

Fishes

As with so many other animals, fishes show considerable flexibility in trophic preferences (Hyatt 1979, Dill 1983). Hagfishes are noted for scavenging behaviour (Hardisty 1979), especially on fishes caught in nets and traps or on lines. They are also frequent scavengers on deep-sea floors. For example, *Eptatretus deani* is a dominant scavenger on the Santa Cruz Basin off California (Smith 1985). Large numbers of this hagfish arrive within minutes after parcels of dead fish are deposited on the deep-sea floor and remain in the vicinity of the bait for hours, even days, until it is consumed.

Predatory sharks may also qualify as the consummate marine vertebrate scavenger but, remarkably, little has been published regarding their natural scavenging activities. Most field studies specifically designed to study scavenging by sharks have involved bait deposited on the deep-sea floor (Dayton & Hessler 1972, Isaacs & Schwartzlose 1975, Desbruyères et al. 1985). Similarly, in shallow water, sharks are either caught or enticed to observers by attracting them with dead bait (Tester 1963, Dodrill & Gilmore 1978, Medved & Marshall 1981, Stevens 1984, Tricas & McCosker 1984, Tricas 1985, Harvey 1989). Laboratory studies on either shark feeding biology or physiology often employ recently-dead meat (Jones 1978, Longval et al. 1982, Frazzetta & Prange 1987, Wetherbee & Gruber 1990). Equipped with acute chemoreceptors (Demski 1982) and a specialized electroreceptor system, comprising numerous ampullae of Lorenzini (Kalmijn 1977, Heyer et al. 1981), sharks can detect either injured or recently-dead animals from considerable distances. Blood and other fluids emanating from fresh carrion attract the sharks, which feed if conditions permit.

There are many predatory teleosts, especially demersal species, which are also facultative scavengers, but few general fish surveys, e.g. Nelson (1984), Wootton (1990) and Sale (1991), acknowledge them. All sportfishes which take bait (despite the obviously deceptive practice of trolling) and a variety of other shallow water species are at least occasional facultative scavengers. Many reef fishes that normally do not scavenge may take either bait or morsels of flesh. On Pacific Panamanian reefs, puffers, especially *Arothron hispidus*, the triggerfish, *Sufflamen verres*, the wrasse, *Thalassoma lucasanum*, the angelfish, *Holacanthus passer* and the damselfish, *Eupomacentrus acapulcoensis* all feed on dead crown-of-thorns sea stars, *Acanthaster planci* (Glynn 1984a). Schools of between 10–20 wrasses were especially effective in breaking up sea stars in the later stages (two days) of decay. Oyster toadfish are lie-and-wait predators by day, but frequently scavenge as they move actively about the bottom at night (Phillips & Swears 1979). Emperor fishes (Lethrinidae) are shallow water marine predators and scavengers of West Africa and the Indo-Pacific region. Aldonov & Druzhinin (1978) describe the distribution and some biological characteristics of several species from the Gulf of Aden.

Many predatory fishes are attracted to a non-living bait by chemoreception. Pinfish, *Lagodon rhomboides*, were attracted to perforated rubber balls containing extracts from

clams, oysters, sea urchins, whelks and shrimps (Carr et al. 1976). Moray eels, *Gymnothorax* spp., could be attracted to chemical extracts of fish, even when vision was experimentally impaired, but less efficiently if external nares were occluded (Bardach et al. 1959). Various natural baits and pure compounds enticed flounders, *Pseudopleuronectes americanus*, mummichogs, *Fundulus* sp., and silversides, *Menidia* sp., to release points (Sutterlin 1975). Glycine was the most effective compound to attract flounders, whereas the other fishes were most easily attracted by L-alanine or L-histidine.

A variety of deep-sea teleosts are frequent facultative scavengers, especially members of the Macrouridae (Pearcy & Ambler 1974, Wilson & Smith 1984, Desbruyères et al. 1985, Priede et al. 1991) and Ophidiidae (Rowe et al. 1986).

Birds

Birds provide us with the best examples of obligate, albeit terrestrial, scavengers. Vultures, e.g. Black vultures, *Coragyps atratus* spp., follow one another from overnight roosts, facilitating foraging efficiency (Rabenold 1987). Food is usually domestic and wild sources of carrion (Coleman & Fraser 1987). Often, a number of species may interact at a carcass, inter- as well as intraspecifically (Wallace & Temple 1987, Hiraldo et al. 1991). Bait experiments suggest that Turkey vultures, *Cathartes aura*, detect bait by smell, preferring fresh and rejecting rotten meat (Houston 1986), although Smith & Paselk (1986) reject rising odorants as a foraging cue.

The time devoted to foraging depends on food availability and soaring conditions (Hiraldo & Donazar 1990), but mean home ranges of Black and Turkey vultures have been determined to be 14881 and 37072 ha, respectively. Such areas usually cover forest and plains, but sometimes include seashores. In 1987, a stranding of 240 Melon-headed whales in north-eastern Brazil attracted vultures (Lodi et al. 1990). A mass stranding of 13 Rough-toothed dolphins in Belize attracted Turkey and Black vultures which stripped them of their skin and eyes (Perkins & Miller 1983). In Costa Rica, Turkey vultures feed at predated Green turtle nests (Fowler 1979).

Whereas terrestrial avian scavengers, notably vultures, visit the marine shore, some typically coastal birds such as Lapwings, *Vanellus vanellus*, and Golden plovers, *Pluvialis apricaria*, forage on agricultural pasturelands (Thompson 1986). Eagles, crows and gulls all scavenge spawned salmon carrion in rivers of the Pacific Northwest (Skagen et al. 1991). The sanderling, *Crocethia alba*, regularly eats parts of the scyphomedusa *Aurelia aurita* stranded on Baltic shores (Grimm 1984). Phillips et al. (1969, p. 709) mention unnamed species of shorebirds as scavengers among the remains of stranded Hydrozoa and Scyphozoa. On sub-Antarctic islands, the Lesser sheathbill, *Chionis minor*, and Southern giant petrels, *Macronectes giganteus*, are opportunistic predators and scavengers of penguins (Hunter 1991). Also in the Southern Ocean, Giant petrels, *M. giganteus* and *M. halli*, are opportunistic predators and scavengers. Both will feed upon either floating or submerged fur seal carrion, with *M. halli* more often feeding upon it than *M. giganteus* (Berutti & Kerley 1985). It is the gulls, however, that are best known scavengers of inland and coastal lands and waters. Gulls naturally feed at almost any intertidal habitat (Pierotti & Annett 1991), most species being opportunistic. Glaucous gulls, *Larus hyperboreus*, for example, feed on a wide variety of plant and animal material (Barry & Barry 1990). Kelp gulls, *L. dominicanus*, join Sheathbills and Petrels to scavenge King penguin chick carcasses (Hunter 1991).

Gulls of many species regularly visit either rubbish tips or landfills (Pierotti & Annett

1991). Three gulls, Herring, *L. argentatus*, Black-headed, *L. ridibundus*, and Great black-backed, *L. marinus*, feed at refuse tips in northeast England where the bigger species and individuals exclude the others (Greig et al. 1985, 1986, Coulson et al. 1987, Monaghan et al. 1986). On the west central coast of Florida, up to 90000 individuals of Herring, Ring-billed, *L. delawarensis*, and Laughing gulls, *L. atricilla*, feed regularly at landfill sites, particularly in the winter (Patton 1988). Western gulls, *L. occidentalis*, nesting on Alcatraz Island in San Francisco Bay, scavenge garbage, their diet being >90% chicken waste (Annett & Pierotti 1989). At Le Havre, on the northwestern coast of France, Herring gulls are fed by local people and exploit rubbish bins (Vincent 1988). Human resources similarly enhanced the population growth of Common gulls, *L. canus*, in the Gulf of Finland. Although numbers have declined in natural populations due to increased predation from other gulls and mammals, solitary pairs which remain near summer cottages have achieved modest protection and food from humans (Bergman 1986). Herring gulls pirate the food of other birds at a New Jersey landfill (Hackl & Burger 1988) and Kelp gulls, *L. dominicanus*, feed on food items of non-marine origin at refuse dumps in South Africa (Steele & Hockey 1991).

Gulls frequently fly far inland for either food or nesting sites. The California gull, *L. californicus*, abandons coastal habitats in the spring, crossing the Sierra Nevada mountains to visit nesting grounds in the vicinity of Mono Lake (Winkler & Shuford 1988). They return to coastal localities in the autumn, where winter populations in some localities are represented in greater densities than most other gulls (Vermeer et al. 1989). In Manitoba, Ring-billed gulls follow tractors cultivating fields to feed on earthworms and grain (Welham & Ydenberg 1988) and linger around haying implements to scavenge either injured or dead grasshoppers, birds and mice. The sight of flocks of gulls over either refuse tips or landfills is matched by them following fishing boats returning to harbour.

On Cape Clear Island, Ireland, Great black-backed gulls scavenge waste from fishing boats (Buckley 1990). Similarly, Shetland Isles whitefish trawlers attract a variety of sea birds, but Great black-backed gulls, Gannets, *Sula bassana*, and Great skuas, *Catharacta skua*, generally outcompete other gulls and Kittiwakes, *Rissa tridactyla*, for most of the discarded whole fish (Hudson & Furness 1989). Fulmars, *Fulmarus glacialis*, generally ignored intact fish discarded from these vessels but their aggression enabled them to monopolize offal. Cory's shearwater, *Calonectris diomedea*, follows motorized boats in the Mediterranean and feeds on fish stunned by propellers (Box 1985). One salty University of Texas boat captain, reflecting on the scavenging prowess of Laughing gulls, refers to the boat-following flocks as "flying feathered sea roaches". Additional aspects of sea birds feeding on trawler by-catch are presented in the section on Human Impacts.

Gulls are well known for their kleptoparasitic habits, i.e. either robbing, scavenging or pirating the food of other birds. Such behaviour uses the time and energy investment of others to reduce the costs of obtaining food (Thompson 1986). Herring gulls kleptoparasitize Common loons, *Gavia immer*, in Rhode Island (Daub 1989); Black-headed gulls, *Larus ridibundus*, rob wintering wading birds in a southern Spanish marsh (Amat & Aguilera 1990) and lapwings, *Vanellus vanellus* (Hesp & Barnard 1989). Herring gulls kleptoparasitize Common puffins, *Fratercula arctica*, returning to their nests from feeding at sea while Heermann's gulls, *Larus heermanni*, do the same to piscivorous Brown pelicans, *Pelecanus occidentalis*, in the Gulf of California, Mexico (Tershy et al. 1990). Kleptoparasitism is not limited to gulls. In the Wadden Sea, The Netherlands, Curlews, *Numenius arquata*, attack conspecifics for food but also fall victim to attacks from gulls (Ens et al. 1990). In North America, Bald eagles, *Haliaeetus leucocephalus*, feed on a variety of prey

and steal food from many other species. They have been observed stealing fish from Greater black-backed gulls and feeding on Coot carcasses (Sobkowiak & Titman 1989).

To avoid kleptoparasitism, Black-tailed godwits, *Limosa limosa*, handle prey underwater when attacked by Black-headed gulls (Amat & Aguilera 1989) while Surf scoters, *Melanitta perspicillata*, reduce thievery by Glaucous-winged gulls, *Larus glaucescens*, in Canada by synchronous diving and surfacing (Schenkeveld & Ydenberg 1985).

Marine mammals

Seals, sea lions, porpoises and other marine carnivorous mammals naturally consume live prey, but captive individuals are usually sustained by a diet of dead fish. Wild Bottlenose porpoises, *Tursiops truncatus*, feed on dead fish discarded from trawlers (Wassenberg & Hill 1990).

Habitats of scavengers and carrion

The majority of animals discussed in the preceding survey are opportunistic scavengers, but the prospect that they will be able to locate carrion and utilize it as a food source is, to some extent, habitat dependent. Carrion readily accumulates in some environments but is less available in others. A complete understanding of carrion and scavenging behaviour thus demands a survey of habitats as well as animals.

Plankton and marine snow

Scavenging behaviour has been little investigated with respect to the marine plankton. A few crustaceans are said to scavenge among the plankton, including some ostracods, e.g. *Conchoecia rotundata* (Alldredge 1972), Cypridina sp. and *Vargula* sp. (Kaestner 1970) and copepods, e.g. *Onacaea mediterranea*, *Microsetella norvegica* and *Paracalanus aculeatus* (Alldredge 1972). Apart from a few mostly anecdotal references, there has been little investigation of scavenging either by or of the plankton, possibly the result of the difficulties engendered in attempting to study interacting planktonic members. There are, however, indications that some of the attributes of successful scavengers, e.g. acute chemoreception, are present among various groups of zooplankton. For example, Antarctic krill, *Euphausia superba*, are suspension feeders, but employ chemoreception of odours, not particles, to trigger feeding behaviour, thereby conserving energy and expending it for feeding only when food is present in high concentrations (Hamner et al. 1983). Almost certainly, scavenging among plankton is more widespread than we have been able to document.

There is one "planktonic" element that, if not actually carrion, effectively mimics it in both form and potential nutritive value. Scattered at all depths throughout the pelagic realm (Silver & Alldredge 1981) are floating microcosms, collectively called marine snow, which arise as amorphous aggregations of organic debris, mucous secretions or nets, diatom frustules, foraminiferan or radiolarian tests, faecal pellets and the gelatinous remains of pelagic Cnidaria, Ctenophora, Tunicata and other invertebrates. Each aggregation of marine snow attracts a variety of nanoplankton and ultraplankton, especially bacteria, fungi, various

phytoplankton, small flagellates and ciliates, many of which derive nutrition from the accumulating mass (Trent et al. 1978, Youngbluth 1985, 1989, Alldredge & Silver 1988, Herndl & Peduzzi 1988). The organic carbon content of marine snow macroaggregates exceeds that of the surrounding water by at least three orders of magnitude (Silver & Alldredge 1981). There is a vast literature on marine snow, but we will focus upon only two aspects here: (a) the concentration of nutrients that, if unaggregated, would likely be either overlooked by or unavailable to pelagic micro- or mesoscalars and (b) the removal by settlement from the water column of nutrients aggregated in marine snow to another community on the sea floor.

New particles of marine snow aggregate rapidly and constantly even as larger, denser, particles are being removed. The high attachment probabilities of suspended macroaggregates suggest that the rate of aggregation of organic particles by physical coagulation in the ocean and its removal from the water column by settling may be many times higher than previously predicted (Alldredge & McGillivray 1991). Once formed, marine snow macroaggregates are highly resistant to disassociation (Alldredge et al. 1990). Although most marine snow aggregates are from 10–20 mm in diameter, particles of up to 90 mm and concentrations of between 2 to 28 aggregates $\cdot l^{-1}$ are not unusual (Trent et al. 1978). Under appropriate lighting conditions, marine snow is readily visible. Thus, a pelagic scavenger of modest size that could detect it either visually or chemically should not be nutrient-limited. We were surprised, therefore, when we were unable to find even one example of a pelagic scavenger reported to feed upon marine snow, although it is often indicated as being an important food source for organisms living below the photic zone (Wiebe et al. 1976, Hinga et al. 1979, Matsueda et al. 1986). It seems unlikely that there is no animal exploiting this resource; more likely that it has yet to be observed and reported upon.

Estimates of the sinking rates of intact marine snow range from about $50 m \cdot day^{-1}$ (Shanks & Trent 1980) to as much as 150 or $200 m \cdot day^{-1}$ (Wells & Shanks 1987, Gooday & Turley 1990). Shanks & Trent (1980) calculated that the sinking of marine snow removed from between 3 to 5% of particulate organic carbon and from between 4 to 22% of particulate organic nitrogen from surface waters each day. If only a fraction of this material reached the bottom, considering the infrequency of large food-falls to the ocean floor, marine snow could provide benthic detritivores with an enormous selective advantage over obligate scavengers. There is increasing evidence that marine snow and other small-sized organic materials move rapidly from their origins near the sea surface to the deep sea floor (Deuser et al. 1981, Matsueda et al. 1986, Graf 1989, Gooday & Turley 1990).

Macro-aggregates originating from the euphotic zone deliver phytodetritus deposits to the deep-sea sediment surface. Although many large deposit-feeding benthic animals consume phytodetritus selectively (Gooday & Turley 1990), its supply is intermittent and often seasonally pulsed. Opportunists able to utilize phytodetritus and other ephemeral food resources such as carrion are, thus, selectively favoured, especially those species capable of withstanding rapid fluctuations in population density (Gooday & Turley 1990, Jumars et al. 1990).

Nekton

Predators dominate the open ocean nekton. Most are non-selective, taking any prey and other food of appropriate size. Scavenging is practised by many upper and mid-water predators, but this is likely to be opportunistic. Virtually all sports fishes (marlin, tarpon,

sailfish, sharks and many others) clearly take dead bait. Yet, the primary food for all of these open water fishes is not carrion, but live prey. In deeper waters, while numerous scavengers can be identified either on or close to the sea floor, most scavenging groups seem to be poorly represented in the water column. For example, a large tuna bait suspended 200m above the bottom at 4850m attracted only a modest number of large mysid scavengers (Rowe et al. 1986). Dahl (1979) maintains that in the pelagic abyss, fish and lysianassid amphipods are the dominant carrion feeders, especially those among the latter which occupy what has been called the "pelagic guild" (Ingram & Hessler 1983, Sainte-Marie 1984).

Deep-sea lysianassids have been divided into two groups, or guilds, based upon body size, foraging patterns and other morphological adaptations (Dahl 1979, Ingram & Hessler 1983). The pelagic guild, represented by species of *Hirondellea* and *Eurythenes*, occupy the water column from near the bottom to many metres above it. There, equipped with acutely sensitive antennule chemoreceptors, they are poised to detect carrion odour plumes emanating from relatively distant points on the deep-sea floor. These amphipods are thus attracted to large pieces of carrion in great numbers (Jumars & Gallagher 1982, Ingram & Hessler 1983). "Notwithstanding their possible predatory rôle in the suprabenthos and pelagos, they appear to be the true necrophage group" (Sainte-Marie 1984, p. 1668).

A second group of lysianassids, the "demersal guild", represented by species of *Orchomene*, are presumed to be less proficient in detecting carrion odour plumes because they rarely rise more than 1m off the bottom. The antennule chemoreceptors of demersal lysianassids are comparable to pelagic guild species (Dahl 1979), so that when the opportunity arises they will also feed upon carrion. A more generalized detritivorous diet, however, probably sustains them (Jumars & Gallagher 1982, Ingram & Hessler 1983). Pelagic and demersal guild lysianassids are additionally distinguished from one another in that the former are larger, more mobile, have significantly greater capacity for internal food storage and have more highly adapted mandibles than the latter.

Sources of carrion amongst the nekton

Regardless of their trophic status, all members of the nekton are potential carrion sources, especially for scavengers of the deep-sea floor. Fishes are undoubtedly the most numerous nekton, but their rôle as potential natural carrion is poorly understood. More often than not, piscivores remove whole prey from the water, leaving no carcass behind to become carrion. In contrast, human fisheries often generate an enormous by-catch of, mostly whole, carcasses either some or much of which is returned to the sea. The importance of by-catch discards to scavengers is discussed in the section on Human Impacts.

Although we have speculated that the death of most marine animals occurs as a result of something other than natural senescence, some cephalopods are apparently an exception. Certain species of shallow-water octopods and squids cease feeding at the onset of the breeding season (Boyle 1983). This fasting usually culminates in death. Although most female octopods succumb in solitary seclusion (Hanlon 1983a, b, Hartwick 1983, Joll 1983, Mangold 1983), the mass mortality of some squids approach, as closely as any animal, the fabled "elephant graveyard". Hundreds, even thousands, of male and female *Loligo opalescens* have been observed lying either dead or dying on the sea floor beneath California spawning grounds (McGowan 1954, Fields 1965). Similarly, a significant number of West Indian hermit crabs, *Coenobita clypeatus*, annually succumb to the rigours of mass migration to the sea, although not entirely the consequence of senescence. On Cayman Brac, B. W. I., one of us (J. C. B.) has observed both the nocturnal migration of *Coenobita*, with

peak densities of migrating animals in excess of $100 \cdot \text{m}^{-2}$ and, the following morning, their carcasses littering a low-relief limestone shore and its tidepools at densities of up to $15 \cdot \text{m}^{-2}$. Marine scavengers likely make use of the seasonal windfalls of cephalopod and crustacean carcasses, but we know of no report in the literature to confirm this supposition.

The larger the nekton body, the more likely some of it will escape ingestion by the original predator. Thus, large fishes, sharks, marine reptiles, cetaceans and other marine mammals constitute a significant quantity of potentially consumable carrion biomass in the sea (Katona & Whitehead 1988). Even terrestrial species, especially sea birds, contribute to the carrion biomass of the water column (Amos 1989).

Schäfer (1972) has summarized much of the data from the first three-quarters of this century concerning the fate of large carcasses in the sea, especially cetaceans. Winn et al. (1987) determined that 18 species of cetaceans comprised an estimated biomass of approximately 25000 tonnes in Georges Bank waters. Similarly, Hain et al. (1985) estimated the biomass of 20 cetacean species from off the northeastern US to be 26506 tonnes. Although cetaceans may be attacked by a variety of predators (Praderi 1985, Norris & Dohl 1980), only a few marine animals, e.g. killer whales and large sharks, are of sufficient size to prey regularly upon most species and then, generally, upon either enfeebled individuals or those smaller than themselves. In a study of the stomach contents of over 6000 sharks, only 1.2% of them contained cetacean remains (Cockcroft et al. 1989). The majority of cetacean biomass may thus not be consumed as living prey. Similarly, only a fraction of the total cetacean biomass comes ashore as beach strandings (Duguy & Wisdorff 1992). We must conclude, therefore, that a considerable quantity of cetacean biomass enters the marine food web as carrion and likely provides nutrient windfalls for a variety of mid-water and, especially, benthic scavengers (Katona & Whitehead 1988). It is likely that other marine nekton contribute proportionally less, depending upon their size and relative abundance.

Deep-sea demersal and benthic scavengers

Most experiments designed to attract deep-sea scavengers employ bait (usually fish), set either within traps or on hooks, to attract a large variety of animals comprising the deep-sea scavenging community. Such a community is generally divided into highly mobile, demersal species, including certain lysianassid amphipods (Dahl 1979), sharks and hagfishes (Isaacs & Schwartzlose 1975), a variety of bony fishes, e.g. macrourids and ophiids (Isaacs & Schwartzlose 1975, Priede et al. 1991) and relatively localized epifaunal and infaunal members including polychaetes, e.g. *Hyalinoecia* sp. (Dayton & Hessler 1972), gastropods, e.g. *Neptunea amianta* (Smith 1985), octopods (Isaacs & Schwartzlose 1975), other lysianassid amphipods (Bowman & Manning 1972, Paul 1973, Hessler 1974, Shulenberger & Hessler 1974, Shulenberger & Barnard 1976, Hessler et al. 1978, Dahl 1979, Thurston 1979, Stockton 1982, Ingram & Hessler 1983, Sekiguchi & Yamaguchi 1983, Vader & Romppainen 1986, Nickell 1989), ophiuroids (Smith 1985) and other echinoderms (see systematic survey). A variety of deep-sea benthic crustaceans in addition to lysianassid amphipods are scavengers, including isopods (Sekiguchi et al. 1982, Briones-Fourzán & Lozano-Alvarez 1991, Tso & Mok 1991) and decapods (Desbruyères et al. 1985).

The vertical zonation of deep sea scavengers between depths of 200–4700 m in the Bay of Biscay was studied by Desbruyères et al. (1985). Decapod crustaceans dominated the scavenger community at depths of between 200–1800 m, while lysianassid amphipods replaced them as the dominant Crustacea at deeper levels. Fish scavengers were most

important below 1800m, with sharks dominating between 1800 and 3000m and demersal bony fishes, especially macrourids, occurring below 3000m. At depths of between 4100–4700m, the collective macrourid biomass was estimated to be between 24–29kg·ha⁻¹, decreasing with depth.

Necrophagy seems to become an increasingly important feeding method with increasing depth (Stockton & DeLaca 1982). Less than seven hours after placing fish bait on the floor of the Philippine Trench at a depth of 9605m, swarms of *Hirondellea gigas* had reduced the intact carcasses to little more than articulated vertebrae (Hessler et al. 1978). At depths of between 3800 to 1800m in the Arctic abyss, *Eurythenes gryllus* is similarly attracted to fish bait (Bowman & Manning 1972, Paul 1973). A baited trap set on the bottom (4855m) in the northeastern Atlantic Ocean caught seven species of lysianassid amphipods; a comparison of species of *Paralicella* and *Orchomene* indicated that the former are specialized necrophages, the latter opportunistic generalists (Thurston 1979). The abundance of these amphipods and other abyssal scavengers, even in some of the least productive regions of the world's oceans (Hessler et al. 1972), suggests that macrophagous scavenging may be more important among the abyssal benthos than once supposed (Sokolova 1972, Dahl 1979, Stockton & DeLaca 1982). Sluggish currents may be the primary means by which the presence of carrion on the deep-sea floor is disseminated to scavengers (Thurston 1979, Smith 1985, Sainte-Marie 1986b, Sainte-Marie & Hargrave 1987). Respiration rates of a shallow-water amphipod, *Orchomene* sp., and the deep-sea species *Paralicella caperesca* and another *Orchomene* were elevated for periods of up to 8hrs when they were exposed to a water-borne odour from bait (Smith & Baldwin 1982), prompting these authors to suggest a metabolic strategy for scavenging amphipods in food-limited environments. They proposed that abyssal scavengers withstand long periods of starvation but are adapted to detect (Dahl 1979, Cocke 1987) and respond rapidly to a food-fall (Hessler et al. 1978). Upon reaching it, they consume a maximal quantity of food in a minimal quantity of time (Hessler et al. 1978), storing it (Holthuis & Mikulka 1972, Shulenberger & Hessler 1974, Dahl 1979, Briones-Fourzán & Lozano-Alvarez 1991) for later efficient assimilation in anticipation of another long wait between meals. Aquarium-held individuals of the giant isopod, *Bathynomus giganteus*, survive as long as eight weeks between feedings (Cocke 1987). Is it, however, either possible or even likely that in such food-limited environments one would find strictly obligate necrophagy? To answer this question we must address the sources and rates of food-falls.

There is little disagreement that large carcasses fall to the deep sea floor, although the frequency of such food-falls must be rare. The natural occurrence of carrion either on or near the bottom has been documented by photographs and, indirectly, by other means. A partially eaten cetacean carcass was photographed on the sea floor at a depth of 3650m from the research vessel ALVIN (Jannasch 1978). A relatively complete skeleton of a seal on the sea floor at a depth of 600m was illustrated by Heezen & Hollister (1971). Other evidence of food-falls include: photographs of dead pelagic scyphomedusae, *Pelagia*, on the sea floor (Shepard & Marshall 1975; Jumars 1976); similar photographs of the bodies of numerous dead salps (Cacchione et al. 1978, Wiebe et al. 1979); the guts of deep sea macrourid fishes containing cephalopod beaks larger than could be obtained by predation (Pearcy & Ambler 1974); and the stomachs of other deep sea fishes containing whale and squid remains (Clarke & Merrett 1972).

There has been much speculation and considerable disagreement as to the importance of large carrion falls, e.g. the carcasses of marine mammals, fishes, cephalopods and cnidarians, to deep sea benthic communities. Some of the initial literature on the subject (Dayton &

Hessler 1972, Grassle & Sanders 1973, Rowe et al. 1974) discounted the importance of such food-falls to the benthos. It was suggested, with some evidence, that large items of carrion reaching the sea floor are located quickly and consumed by highly mobile, mostly either nektonic or demersal scavengers, especially fishes and lysianassid amphipods, which effectively deny most of the nutrient windfall to the local benthos. If the carrion is not located and consumed by necrophagous scavengers, deep-sea bacteria react quickly to decay it (Sieburth & Dietz 1972, Gooday & Turley 1990).

Stockton & DeLaca (1982) pointed out that deep-sea scavengers, especially highly mobile species, are likely made aware of and attracted to a food-fall by solutes leaching from it. They suggested that the threshold detection level of chemical cues is probably related to the speed at which the organism can move and that "a slow moving organism should respond only to food-falls that are nearby and have a relatively undiluted odor" (p. 162). For example, slow-moving, benthic subtidal nassariid scavengers have less acute chemosensory reception than their intertidal counterparts (Britton & Morton 1993b, Liu & Morton 1994). This could account, at least in part, for the sparse assemblage of local benthic scavengers attracted to relatively small baits lowered to the deep sea floor.

After the initial wave of pessimism, subsequent investigations began to dispute the assertion that large food-falls had little impact upon the local benthos. Stockton & DeLuca (1982) suggested that, despite their rarity, large food-falls represent significant environmental perturbations with potentially long term influences, both directly and indirectly, on such aspects as local faunal diversity, composition and biomass. In relation to the normally low rates of energy input and respiration on most deep sea bottoms, a single, albeit rare, large food-fall represents a massive localized energy enrichment that is not entirely removed by mobile scavengers. Parcels of dead fish placed on the sea floor of the Santa Catalina Basin attracted aggregations of demersal fishes, but also the infaunal ophiuroid *Ophiophthalmus normani* in densities as high as $700 \cdot \text{m}^{-2}$ (Smith 1985). Benthic standing-crop and turnover-rate estimates for these baits indicated that perhaps 11% of benthic community respiratory requirements were met by nekton carcasses reaching the sea floor (Smith 1985). In the process of feeding, fish and ophiuroid scavengers significantly disrupted sediments on the sea floor, causing a localized reduction in infaunal species diversity and abundance (Smith 1986). Such observations cannot be interpreted as insignificant impacts on the local deep sea benthic community.

Stockton & DeLaca (1982) further hypothesize (without corroborative data) that the nutrient value of a deep-sea food-fall may have a greater enrichment impact on the adjacent benthic community not as carrion, but as faecal discharge from its scavengers, with a broad area surrounding the food-fall benefiting from such enrichment. The sea floor could thus be envisioned as a mosaic of small, localized, nutrient-enriched areas separated by broad, expansive, oligotrophic deserts. Each enriched element of the mosaic begins at a food-fall focus with the majority of the nutrients removed from the scene by mobile scavengers, but at least some utilized directly by slower-moving components of the benthos. All scavengers expand the initial area of enrichment by faecal deposition. The local benthic community, in turn, responds for a time to secondary enrichment, until its nutritive value is eventually depleted, at which point the once-enriched site returns to its background level of oligotrophy. The analysis by Smith (1986) of a Santa Catalina Basin community in which benthic diversity and community abundance decreased near a food-fall as a result of environmental disturbance by the initial scavengers contradicts the Stockton-DeLuca model.

Recently, the importance of food-fall dispersal by deep sea demersal fishes has been re-evaluated by use of sophisticated electronic and photographic surveillance equipment

(Priede et al. 1991). In particular, two closely related demersal fishes, *Coryphaenoides armatus* and *C. yaquinae*, were found to be active foragers capable of moving independently of bottom currents and affecting significantly bait dispersal at depths of between 4000 and 6000m.

The considerable mobility of large baleen whales from highly productive feeding grounds to nutrient-poor tropical waters also ensures that some of this enormous cetacean biomass will fall upon otherwise impoverished deep-sea benthic communities providing, albeit temporary, localized, nutrient enrichment to the benthos (Whitehead & Moore 1982, Katona & Whitehead 1988). The precipitous decline in cetacean numbers due to overfishing during the last two centuries may also have had consequences for deep sea benthic communities.

If, as suggested by Smith (1985), nekton carcasses reaching the sea floor account for perhaps 11% of benthic community respiratory requirements, something other than food-falls must provide the primary sustenance for the "scavengers" of these communities. Just as opportunism presents a serious pitfall in the reconstruction of palaeoecological food webs (Cadée 1984), so must it also present a difficult problem in interpreting trophic relationships in an oligotrophic community lacking primary producers and relying upon the highly unlikely chance encounter that nutritive mana will fall nearby. Any species which must rely on scavenging a carrion meal in such an environment to the exclusion of all other nutrient sources must be at a selective disadvantage, but any species capable of locating and supplementing its diet with an occasional carrion windfall has a distinct advantage. The growing realization that other nutrient sources, i.e. marine snow, phytodetritus and similar small-sized organic inputs, move rapidly from the photic zone to the deep-sea floor (Deuser et al. 1981, Matsueda et al. 1986, Graf 1989, Gooday & Turley 1990), also suggests that opportunistic necrophagous scavenging might supplement an otherwise detritivorous diet for many deep-sea animals.

Shallow shelf habitats

Subtidal shelf habitats are among the earliest known marine environments documented in the fossil record. The remains of an ancient (530 mybp) subtidal benthic community were preserved in the Burgess Shale, including several suspected scavenging arthropods (Conway Morris & Whittington 1979, Conway Morris 1986). A variety of scavengers also occupy modern shallow subtidal communities but, so incompletely known are the diets and feeding behaviours of most species that, except for the few we have recognized either here or in the faunal survey, many are yet to be identified.

The more successful scavengers of the shallow sea floor, especially fishes, amphipods and a few isopods, are fast and agile (Sainte-Marie & Hargrave 1987, Briones-Fourzán & Lozano-Alvarez 1991). Experiments to detect subtidal scavenging have been of two types: (a) those in which fish have been included and (b) those in which fish were either deliberately or mistakenly excluded. In the former case, fish are identified as the dominant carrion consumers (Dayton & Hessler 1972, Hessler & Jumars 1974, Wilson & Smith 1984, Smith 1985). When baited pots placed upon shallow subtidal bottoms exclude fish, a suite of what would normally be secondary arrivals is recorded. Thus, Eriksson et al. (1975) indicate that "important" subtidal scavengers from Gullmar Fjord, Sweden, were *Carcinus maenas*, *Pagurus bernhardus*, *Crangon vulgaris*, *Asterias rubens* and *Nassarius reticulatus*. It seems possible that the accidental exclusion of fish may misrepresent this scavenging community. Observations by Hill & Wassenberg (1990) on unprotected baits set on the shelf bottom

showed that nemipterid teleosts and sharks ate most of it; in this case, invertebrate scavenging was negligible. *Buccinum undatum* has long been regarded as a scavenger because it is taken regularly in baited traps (Dakin 1912). Nielsen (1975) and Taylor (1978) have, however, demonstrated that *B. undatum* is primarily a predator of bivalves and polychaetes, scavenging only opportunistically. *Oliva sayana* of the southeastern US, though a predominantly polychaete predator, feeds on fish carrion when it is present (Kohn 1961). Similarly, *Carcinus maenas* is now regarded as a significant predator of cockles, *Cerastoderma edule*, in European waters (Sanchez-Salazar et al. 1987a, b), and its reported significance as a scavenger is, in reality, a consequence of both opportunistic behaviour and faulty experimental design. The same is true of *Asterias rubens*, naturally a predator of bivalves, polychaetes, barnacles and other living invertebrates (Jangoux 1982).

A variety of shallow subtidal amphipods feed on carrion, including representatives of some unlikely groups such as Gammaridae, e.g. *Gammarus deubeni* (Kinne 1959) and Caprellidae, e.g. *Paracaprella tenuis* (Caine 1974). As in the deep-sea, lysianassid amphipods are important scavengers of shallow subtidal and intertidal habitats. Like their deep-water counterparts, shallow-water lysianassids have well-developed antennule chemoreceptors that enable some species to detect a scent from carrion as much as 30m away (Bushdosh et al. 1982). Some species also appear to be better adapted for scavenging than others (Sainte-Marie 1984). *Anonyx sarsi* and congeners have some of the morphological adaptations similar to those of deep-sea, pelegic-guild, lysianassids that make them better suited for necrophagy. Others, such as *Onisimus littoralis*, *Orchomenella pinguis* and *Psammoneyx nobilis*, although feeding upon carrion when it is available, more appropriately represent a group of shallow-water scavenging omnivores. Penaeid shrimps were suspected of being major scavengers of discarded by-catch from Gulf of Mexico trawlers (Flint & Rabalais 1981, Sheridan et al. 1984), but direct observations in Australian waters produced no evidence of penaeids feeding on trawler discards (Wassenberg & Hill 1987).

Necrophagy has been cited as an important adaptive feeding strategy among several groups of subtidal Antarctic invertebrates (Arnaud 1977). Several species of turbellarians (Dayton et al. 1974), asteroids (Jangoux & Lawrence 1982), ophiuroids (Arnaud 1974) and pycnogonids (Arnaud 1972, Arnaud & Bamber 1987) are frequent scavengers on Antarctic shelf sea floors.

Soft-substratum beaches

On sandy beaches, natural water movements assure that chemical cues arising from carrion will be dispersed. Food detection by chemoreception is enhanced considerably when currents impose directional gradients (Carthy 1958). Tidal incursions (aided by waves) both assist and hamper an intertidal scavenger's search for food. Potential food is brought onto the beach as allochthonous flotsam by the tide, waves and longshore drift, thereby enhancing the natural productivity of the shore (Madden 1987). With time, it may be lifted up, moved upshore and stranded, where it is unavailable to most marine scavengers. As the stranded flesh decomposes, either a subsequent tide or wave backwash may return it to the sea to begin the cycle again. Beached carrion is probably, therefore, a highly ephemeral resource, requiring many tidal incursions and exchanges before it is consumed.

Water flow on a low-relief, sheltered, beach is less likely to disperse olfactory signals than the turbulent flow on a wave-swept rocky beach (Lubchenco & Menge 1978, Britton & Morton 1992). The former environment, therefore, usually harbours a greater number and

variety of marine scavengers than the latter. Flowing water on a beach may be the result of: (a) the broad, regular, predictable tidal flux; (b) the directional discharge of either springs or streams; or (c) lapping waves which serve to extend the time over which a chemical cue is kept water-borne. Because a gentle slope is usually characteristic of sandy beaches experiencing minimal wave energy, chemical cues emanating from stranded carrion are thus (i) concentrated in receding water and (ii) directional; both, however, facilitate the food-finding process.

On shores with a considerable tidal range, chemical cues, while subjected to potentially greater dilution, are transported greater distances during a falling tide than on shores where the tidal range is narrow. Scavengers on these beaches often repose either on or, more often, within the more protected substratum of the mid- and lower intertidal, being assured of receiving chemical messages when food arrives up-shore, but avoiding desiccation, temperature extremes, predation pressures and other hardships which characterize the higher shore. The gentle flow of each falling tide transports chemical cues down tidal flats, alerting reposing scavengers to two kinds of potential food: (a) carrion washed in by the last high tide and stranded during the current falling tide and (b) either dying or recently moribund denizens of the upper shore which have succumbed to the natural stresses which characterize such an environment. These two kinds of food are frequently cited as the focus of feeding intertidal scavengers, e.g. *Ilyanassa obsoleta* in the Western Atlantic from New Brunswick, Canada to northern Florida (Scheltema 1964), *Nassarius reticulatus* from the Eastern Atlantic (Tallmark, 1980), *N. pauperatus* from South Australia (McKillup & Butler 1979, 1983), *N. pyrrhus* from Southwest Australia (Morton & Britton 1991), *N. festivus* from Hong Kong (Morton 1990, Britton & Morton 1992), *N. luteosoma* from the western coast of Costa Rica and *N. tiarula* from the Gulf of California (Houston 1978). Each cited species scavenges upon intertidal flats under the conditions just described.

When food is present, gastropod and hermit crab scavengers frequently move to higher parts of the shore to feed. This may occur either on rising or, more commonly, on falling tides. This is in contrast to most marine predators which occupy the upper shore during high tides and retreat to deeper water during low tides (Paine 1966, Louda 1979). Scavengers are usually among the common invertebrates observed on broad intertidal flats which otherwise afford little protection against terrestrial predators such as birds (Reese 1969). Thus, scavengers of intertidal flats often encase their bodies within thick, predator-resistant, shells which also provide some degree of protection to environmental extremes encountered during feeding excursions. Species occupying temperate climates may move off intertidal flats in winter and return in spring, often in mass migrations, e.g. *N. reticulatus* (Tallmark 1980) and *Ilyanassa obsoleta* (Crisp 1969, Borowsky 1979, Brenchley 1980).

Some intertidal gastropod scavengers have different adaptations which enable them to succeed upon sand beaches with a broad tidal amplitude and moderate to high wave energy. *Bullia rhodostoma*, *B. vittata*, *B. melanoides*, *B. natalensis* and *B. pura* are intertidal nassariids of the Southern Ocean (South Africa) which, like *B. digitalis*, employ a broad, thin, foot like a sail, surfing either up or down the beach (Ansell & Trevallion 1969, Brown 1971, McLachlan et al. 1979). The behaviour is similar to that reported for *Hastula salleana*, a terebrid carnivore from Gulf of Mexico sandy beaches which feeds upon intertidal polychaetes (Kornicker 1961). *Bullia* spp. employ such behaviour for diurnal migrations up and down the beach, in part, at least, to access carrion (Brown 1982).

Invertebrate intertidal scavengers on shores of limited tidal range are often restricted to arthropods, especially hermit crabs, amphipods and isopods (Reese 1969, Britton & Morton 1993a). Gastropod scavengers, if not absent, occur in low numbers on these shores. For

example, despite a suitable substratum and being relatively well-protected from strong wave action, the shores of the western Gulf of Mexico lack significant populations of intertidal gastropod scavengers. Even hermit crabs, e.g. *Clibanarius vittatus*, rarely occur in dense aggregations. The tidal range is narrow throughout the western Gulf region, generally <0.5 m. As a result, intertidal scavengers would be limited to an extremely narrow zone of repose. Chemical cues, rather than flowing gently down a broad tidal flat, are quickly captured by long-shore currents and swept away. The importance of shore geomorphology to intertidal scavenging behaviour is difficult to evaluate empirically but, these observations suggest that, with the exception of the surfing nassariids of the Southern Ocean, a broad tidal range on a sheltered beach of unconsolidated sediments facilitates intertidal scavenging.

Beached carcasses of marine mammals may be consumed by terrestrial scavengers. Polar bears, *Ursus maritima*, and Arctic foxes, *Alopex lagopus*, scavenge stranded cetacean and pinniped carcasses (Katona & Whitehead 1988). California condors may have survived in coastal regions after the disappearance of the Pleistocene megafauna by scavenging the remains of beached marine mammals (Emslie 1986). Mass strandings of Rough-toothed dolphins, *Steno bredanensis*, in Belize and Melon-headed whales, *Peponocephala electra*, in Brazil both attracted vultures (Perkins & Miller 1983, Lodi et al. 1990).

Hard shores

An exposed hard shore is not especially suited to accumulate carrion. Useful olfactory cues are disrupted by turbulent flow on wave-swept rocky shores (Dayton 1971, Lubchenco & Menge 1978, Louda 1979, Sloan 1980). Under these conditions, successful scavenging seems primarily dependent upon fortuitous encounters (Menge 1972, Dayton et al. 1977), but small pieces of carrion sometimes become trapped between rock crevices. A few hard shore species are capable of exploiting it. Several actinarians will grasp bits of carrion with their tentacles and ingest it opportunistically. Most rocky habitat communities include other potential scavengers, e.g. mainly carnivorous turbellarians, nemerteans and polychaetes that take carrion if it is presented to them. Perhaps the best known scavengers of rocky shores are arthropods, especially isopods, e.g. the cosmopolitan, omnivorous *Ligia* spp. and *Cirolana hartfordi* from rock-strewn sandy beaches of western North America (Johnson 1976a, b), and some decapods, e.g. *Geograpsus stormi*, from Indo-Pacific rocky shores (Gilchrist 1988). The intertidal gastropod, *Searlesia dira*, although mostly carnivorous, occasionally feeds upon carrion (Louda 1979). Similarly, the predatory *Thais orbita* (= *Dicathais aegrota*) feeds on carrion and comes to bait on intertidal rock platforms in Western Australia (Phillips 1969, Morton & Britton 1993).

Reefs

Carrion is normally an unusual commodity on tropical coral reefs, probably as a result of the diversity of animals ready to consume any available morsel. The sea urchin broken by a diver's knife is attacked immediately by a variety of reef fishes and consumed rapidly. Any exposed, enfeebled, animal is either quickly reprocessed by members of the reef community or whisked out of it by pelagic predators such as sharks. Glynn (1984a), however, describes predation by an amphinomid polychaete on the crown-of-thorns sea star, *Acanthaster planci*, which results in a high percentage of either wounded or moribund asteroids which are

subsequently attacked by a suite of at least twelve vertebrate and invertebrate scavengers on Pacific Panamanian coral reefs. Glynn found the number of species feeding on *Acanthaster* and the attack and processing rates by predators and scavengers higher in Panama than in either Samoa or Guam. Dead *Acanthaster* were usually picked clean and disintegrated, especially by wrasses, *Thalassoma lucasanum*, within four days of death. Trophic relationships amongst the cryptofauna of coral reefs, e.g. Rasmussen & Brett (1985), Kobluk (1988) and Morton et al. (1991), are poorly understood, but some facultatively scavenging members are likely present.

Most of the focus on death and decay of coral reef communities has been with geological processes such as reef diagenesis (Ginsburg 1957, Land 1967, James 1974, Constantz 1986), taphonomy (Scoffin 1992) and, most recently, the consequences of natural disasters brought about by either disease (Lessios 1988) or environmental stress (Williams & Bunkley-Williams 1990).

The 1983–84 mass wasting of tropical Atlantic populations of the Long-spined sea urchin, *Diadema antillarum*, apparently as a result of a host-specific pathogen, precipitated a number of papers which considered the short- and long-term impacts of the loss of this herbivore on reef ecosystems (Lessios 1988 provides a comprehensive review). Except for a few anecdotal remarks in some of the early reports, e.g. Laydoo (1984) and Lessios et al. (1984), however, little information was provided as to the immediate fate of the *Diadema* carrion windfall during the die-off except that, apparently, the pathogen was not transmitted to any scavenger feeding upon the moribund tissue.

There is also a considerable body of literature documenting mass mortalities of either marine populations or ecosystems as a result of environmental stress (Woodley et al. 1981, Glynn 1984a, b, Brown 1987, Morton & Britton 1993 and additional references cited in the section on Human Impacts). With an eye to the future, perhaps the most distressing environmental perturbation with respect to coral reefs is the mass mortality of hermatypic scleractinians and associated organisms in response to hyperthermal stress. Coral mortality is preceded by "coral bleaching", as zooxanthellae succumb to excessive water temperatures (Williams & Bunkley-Williams 1990, Glynn 1991). Some authors attribute this phenomenon to global warming and have expressed concern that it may accelerate. There are no reports, to date, that this type of coral mortality benefits reef scavengers. If hyperthermal coral mortality becomes widespread, however, reef scavengers might be one benefactor of this potential tragedy.

A variety of facultative scavengers frequent oyster reefs. The oyster parasite, *Perkinsus marinus*, survives passage through the digestive tracts of many of these species, such as the crabs *Callinectes sapidus*, *Panopeus herbstii* and *Eurypanopeus depressus* and the fish *Gobiosoma* sp. By feeding upon either dying or recently deceased infected oysters, these scavengers serve as important vectors, spreading the parasite to new portions of an oyster reef (Meyers & Bureson 1989).

Coastal wetlands and grass beds

Mangroves, salt marshes and subtidal grass beds are largely the domain of herbivores, detritivores and suspension feeders. A large variety of arthropods (amphipods, isopods, cumaceans, decapods and many others) process leaf litter produced by the vegetation dominating these habitats. Vegetative detritus overwhelms the deposition of carrion to such a profound degree that a carrion-feeder would usually be at an extreme disadvantage. Some

predatory mangrove crustaceans, e.g. the portunid *Scylla serrata* of the Indo-Pacific, are certainly facultative scavengers, the method of commercial harvesting being by baited tangle nets (Melville & Morton 1983). Similarly, *Chicoreus* (= *Murex*) *pomum* is a molluscan predator (Radwin & Wells 1968) of various subtidal habitats, including tropical turtle grass beds, where one of us (J. C. B.) has observed it feeding on fish carcasses.

Detecting carrion: chemoreception

Chemoreception is used by marine organisms in a variety of ways, including predator recognition and the possible consequential adoption of either behavioural avoidance reactions or production of defensive secretions, establishment of symbiotic associations, reproductive activities and detection of and/or orientation towards food (Mackie & Grant 1974, Kohn 1983, Croll 1983). Decomposing carrion gives off a variety of chemical cues and it is, presumably, these substances that attract macrophagous scavengers to such moribund food, although some may also utilize visual cues. Chemoreception is not, however, the exclusive domain of scavengers, for predators and herbivores alike can be attracted to food by chemical stimuli. For example, piscivorous species of *Conus* may become active when a live fish is introduced into an aquarium (Kohn 1956). Many predatory opisthobranchs employ chemosensory receptors to stalk their prey (Cook 1962, Waters 1973, Willows 1978). Similarly, when the green alga, *Ulva lactuca*, (or when water in which *U. lactuca* has been held) is introduced into an aquarium containing the Hawaiian sea hare, *Aplysia juliana*, the latter orients towards the introduction site (Frings & Frings 1965). The basis for food detection by chemoreception, therefore, is well founded among animals and requires only some degree of focus, according to specific food preferences (Lindstedt 1971, Lenhoff & Lindstedt 1974). Macrophagous scavengers apparently focus upon chemical cues normally not released by living prey.

The feeding behaviours of scavengers are usually complex, involving several sequential steps. Kohn (1983) described a feeding sequence for many gastropods which is also appropriate for many macrophagous invertebrate scavengers. Chemical cues alert scavengers to the presence of a potential food and elicit arousal behaviour. This is usually followed by orientation and eventual locomotion toward the perceived food source. Processing and consumption may commence either immediately upon arrival at the food or may be preceded by exploratory behaviour. As we will demonstrate, the duration of feeding may also follow a predictable behavioural sequence, related either to the degree of hunger or satiation and to other intrinsic factors.

Chemical cues which elicit arousal behaviour may be the result of either direct physical contact with the potential food or delivered from a distance by the intervening seawater medium. The relationship between chemoreception and foraging behaviour in crustaceans has been reviewed by Zimmer-Faust (1989). Contact chemoreceptors on several appendages of the horseshoe crab, *Limulus*, elicit strong electrophysiological responses when stimulated by aqueous extracts of marine bivalves, yeast and beef (Barber & Hayes 1963). In the decapod Crustacea, food searching consists of two components: near field (non-locomotor leg and chelae probing) and far-field search (locomotion) (Zimmer-Faust 1982). The mangrove crab, *Scylla serrata*, for example, forages over an average distance of 480m, usually at night (Hill 1978), but locates food by contact chemoreception using the dactyls of the walking legs (Hill 1979). The hermit crab, *Clibanarius vittatus*, initiates feeding behaviour

when antennule receptors detect certain chemical stimuli carried in fluids extracted from recently-killed fish (Hazlett 1968). The same species also locates new gastropod shells (and possibly food scraps) from a distance underwater by molecules released from gastropod flesh during predation events by species of *Busycon* (Buccinidae) (Rittschof et al. 1990). Chemoreceptor cells are abundant on the anterior margin of the foot, the tips of the cephalic tentacles and the ventral external surface of the siphon of *Nassarius reticulatus* (Crisp 1971, 1976). Direct application of crab extract to the anterior border of either the foot or tentacles elicited a feeding response more often than when either the siphon tip or posterior foot of *N. reticulatus* was stimulated (Crisp 1971). Similarly, the application of various food extracts and amino acids to the leading propodial edge of *Bullia digitalis* stimulated proboscis eversion whereas amines applied to the same location did not (Hodgson & Brown 1985, 1987). Contact chemoreception may trigger an immediate feeding response by the detecting organism which is already in close proximity to the food. This is a desirable situation for herbivores and detritivores which forage in intimate proximity to a variety of potential foods – some of which are likely either more palatable or nutritious than others (Lubchenco 1978). Contact chemoreception is, however, generally ineffective in alerting scavengers to remote but accessible food. In this instance, distance chemoreception comes into play.

Distance chemoreception has been best studied in echinoderms, gastropod molluscs and fishes. Sloan & Campbell (1982) provide an extensive review of chemoreception in the Echinodermata. For example, *Luidia clathrata* responds most strongly to L-cystine, L-isoleucine and L-glutamic acid compounds emanating from fleshy animal foods (McClintock et al. 1984). Hara (1982) and Klaprat & Hara (1984), respectively, provide a review and a bibliography of chemoreception in fishes.

Kohn (1961) reviewed much of the earlier literature and concluded that distance chemoreception was the most important means of food detection among carrion-eating gastropods. The osphradium is usually implicated as the primary site of distance chemoreception associated with food recognition and location (Brown & Noble 1960, Kohn 1961). Active macrophagous gastropod scavengers and predators generally have larger, more elaborate, osphradia than either herbivores or predators seeking sessile prey (Taylor & Miller 1989).

Many substances are now known to be important stimuli of distance and contact chemoreceptors in gastropod scavengers. A variety of proteins, including those from human blood plasma, fluids and extracts from oysters, scallops, other bivalves, the blue crab *Callinectes sapidus* and fishes, induce a strong feeding response in *Ilyanassa obsoleta* (Gurin & Carr 1971, Carr et al. 1974). Trimethylamine, emanating from carrion, stimulates chemoreceptors on the osphradium of *Bullia* sp. (Brown & Noble 1960). When trimethylamine and other volatile amines are brought into contact with the osphradium, *Bullia digitalis* commences food-searching behaviour (Brown 1971). *Ilyanassa obsoleta* also follows the mucous trails of conspecifics and those of *Nassarius vibex* towards food (Trott & Dimock 1978). When crushed conspecifics are presented to *Ilyanassa obsoleta*, however, an alarm response and escape reaction ensues (Atema & Burd 1975) that is only overcome by extreme hunger (Stenzler & Atema 1977). Similarly, the tidepool Sculpin, *Oligocottus maculosus*, responds to chemical cues released from injured conspecifics (Hugie et al. 1991).

Reports of gastropods sensing carrion from distances of between one to several metres are common, especially with respect to intertidal nassariids (Copeland 1918, Morton 1960, Bedulli 1976, Morton 1990, Morton & Britton 1991, Britton & Morton 1992). Large subtidal buccinids can detect bait from many metres (Gros & Santarelli 1986). The record for distance chemoreception by a gastropod, however, must be the observation by MacGinitie

& MacGinitie (1968) who reported witnessing *Nassarius fossatus* moving upstream toward a dead fish from a distance of more than 30 m. Deep-sea scavengers, particularly lysianassid amphipods and fishes, are attracted from significantly greater distances than those reported for shallow-water and intertidal scavengers (Sainte-Marie & Hargrave 1987). The bathyl isopod *Bathynomus giganteus* also seems to be attracted to carrion by chemical rather than visual cues (Chamberlain et al. 1986, Cocke 1987).

Upon sensing potential food, most gastropod scavengers commence moving towards it. Sand-dwelling species, especially nassariids, emerge from the substratum, sweep the siphon across the direction of water flow and, generally, move toward the food, e.g. *Ilyanassa obsoleta* (Carr 1967a), *Bullia rhodostoma* and *B. digitalis* (Brown 1982), *Nassarius festivus* (Britton & Morton 1992) and *N. pyrrhus* and the buccinid *Cominella eburnea* (Morton & Britton 1991). The effectiveness of their movement toward the food is dependent on the current patterns sweeping around it and either the strength or dilution of the chemical stimulus (Britton & Morton 1992).

The speed by which gastropod scavengers move towards food in the presence of an uninterrupted chemical stimulus varies according to the species, but is usually rapid. Gros & Santarelli (1986) recorded a mean speed of $20 \text{ cm} \cdot \text{min}^{-1}$ for *Buccinum undatum* moving upstream toward a baited trap while Morton (1990) has shown that the subtidal *Babylonia lutosa* (Buccinidae) was relatively slower at reaching food than the intertidal *Nassarius festivus*. Morton & Britton (1991) have shown that the intertidal *N. pyrrhus* took a mean time of 8.45 min to find food placed 20 cm away, whereas the predominantly subtidal *Cominella eburnea* took 18.9 min. All individuals of *Nassarius pauperatus* that responded to bivalve bait, *Katelysia scalarina*, made available to field populations usually arrived at the bait within ten minutes of it being set out (McKillup & Butler 1983). The rate of locomotion in *Ilyanassa obsoleta* is correlated negatively with size (Dimock 1985).

Bullia digitalis is, perhaps, the fastest moving nassariid, utilizing a unique means of locomotion apparently evolved as an adaptation to its wave-swept sandy beach habitat. This snail relocates either up or down a shore by extending and spreading its broad foot and allowing waves to transport it (Brown 1971). Surfing activity is employed for both diurnal and tidal migrations and in response to chemical cues revealing the presence of carrion (Trueman & Brown 1976, Brown et al. 1989).

Lobsters, *Homarus americanus*, orientate within a turbulent odour plume and Sainte-Marie & Hargrave (1987) suggest that patterns of arrival, times of first arrival on bait and instantaneous numbers of individuals on bait can be used to estimate abundance and distance of attraction for scavenging species of fish and invertebrates. A simple Gaussian plume model was used, which takes into account the rate of odour production by bait, the chemosensory threshold of scavengers, their swimming speed relative to current velocity and satiation time. Information about many of the parameters and assumptions which are critical to the model are, however, lacking.

Consumption and energetics

Unlike a predator which has to subdue and gain entry to its prey, a scavenger does not have the energetic expenses involved in these two processes. The scavenger has only to detect and find the food. Thereafter, consumption is immediate and provides an energetic value equal to that of living prey. However, species which rely upon a diet of carrion face two

major disadvantages. The availability of carrion in the marine environment, except in the cases of regular trawler discards, is usually infrequent and, when present, it is usually not so for long. Physical forces such as tides and currents may remove it from the vicinity, bacterial decay may render it increasingly less palatable for some scavengers and, perhaps, most important, other scavengers, either conspecifics or other species, are competitors for the same resource. It follows, therefore, that the energetic advantage of carrion is lost if it is not exploited immediately and to the full. Thus, in the presence of a bait odour, oxygen consumption rates in both *Nassarius reticulatus* (Crisp et al. 1978) and two species of deep-sea amphipods (Smith & Baldwin 1982) are elevated dramatically, a physiological adaptation that facilitates them to arrive at food quickly.

The most efficient scavengers have acute powers of chemoreception, e.g. nassariid gastropods (Carr 1967a, b, Crisp et al. 1978) and lysianassid amphipods (Dahl 1979). Gastropod scavengers move towards carrion purposefully at speed. *N. festivus* can arrive at food from a distance of ~ 2.5 m (Britton & Morton 1992). Notwithstanding, individuals arriving from this distance rarely consume an average bivalve meal because most has already been eaten by closer conspecifics. As with nassariid gastropods, deep-sea scavenging amphipods, i.e. *Paralicella caperesca* and *Orchomene* sp., respond dramatically to the odours emanating from carrion by elevating oxygen consumption rates (Smith & Baldwin 1982). They do not, however, arrive at bait so quickly. Ingram & Hessler (1983) and Hargrave (1985) both report the first appearance of *Eurythenes gryllus* 4 h after the establishment of bait and subsequent rates of arrival of < 5 individuals $\cdot$ h $^{-1}$.

Scavengers which are first to arrive at carrion often eat to engorgement. Many deep-sea lysianassid amphipods have enlarged digestive tracts to accommodate storage of a greater quantity of food (Dahl 1979), as do species of the large isopod *Bathynomus* (Briones-Fourzán & Lozano-Alvarez 1991, Tso & Mok 1991). One hundred g of mackerel moored 20 m above bottom at 5830 m in the Nares Abyssal Plain of the Northwest Atlantic Ocean, was consumed by scavenging lysianassid amphipods, *Eurythenes gryllus*, within 38 h (Hargrave 1985). The mean feeding time was $30 \text{ min} \pm 10 \text{ min} \cdot \text{individual}^{-1}$, with an average consumption rate of $2.9 \text{ g} \cdot \text{individual}^{-1}$. Each amphipod ingested between 30 to 60% of its body weight and then departed from the bait. Such rates are consistent with other observations of rapid bait consumption by lysianassid amphipods and a consumption of $< 150\%$ of body dry weight of fish flesh in one feeding bout by *E. gryllus* (Meador 1981). Total ingestion $\cdot$ individual $^{-1}$ for *E. gryllus* would provide between 1260–18500 calories which would sustain respiration for between 84–142 days. Taken together, a single feeding to satiation and utilization of all body lipid reserves would support basal metabolic rate in *E. gryllus* for between 3–5 months. Maximum meal size of the estuarine amphipod, *Anonyx sarsi*, ranged from 29 to 37% of net dry body weight, increasing with absolute body size and decreasing with increasing sexual maturity of females (Sainte-Marie 1987).

Gastropod scavengers demonstrate similar feeding energetics. Most nassariids feed quickly on carrion, with feeding duration sometimes mediated by the time since the last meal (Crisp 1978). Buccinids feed longer and seem less likely to alter the duration of feeding based upon the last meal. *Bullia digitalis* has been reported to ingest up to one-third of its own tissue weight in food during ten minutes of feeding (Brown 1961). Morton (1990) found the mean time spent on fish carrion by *Nassarius festivus* to be ~ 8 min after ten days of starvation, but about half that time when fed one day after a previous feeding. In contrast, the mean time spent on fish carrion by *Babylonia lutosa* was ~ 15 min whether either 1 or 10 days had elapsed following a meal, although the variance was considerably greater after 10 days starvation. Morton & Britton (1991) described a similar relationship for *Nassarius*

pyrrus and *Cominella eburnea* from Southwest Australia. The former arrived at food first and departed after feeding for ~6 to 7 min; the latter arrived about the time most nassariids were departing and fed for considerably longer. Subtidal *Nassarius mendicus* spends ~7.5 min feeding on fish carrion, ingesting 1.69 ± 0.24 mg dry weight fish tissue $\cdot$ feed⁻¹, but almost 13 min feeding on bivalve tissue, ingesting 0.45 ± 0.26 mg dry weight bivalve tissue $\cdot$ feed⁻¹ (Britton & Morton 1993b). The mean time spent feeding by *N. mendicus* decreased with the number of times an individual fed over a period of 9 days, and the mean time between meals for all individuals feeding more than once was 3.14 days. Oxygen uptake increases immediately when *N. reticulatus* either feeds or is exposed to food odours (Crisp et al. 1978).

Morton & Britton (1991) showed that *N. pyrrhus* could consume ~21% of its dry body weight in an average feeding bout of 6.75 min, i.e. ~3% $\cdot$ min⁻¹. Morton (1990) has shown that, in Hong Kong, *N. festivus* consumes ~50% of its body weight $\cdot$ day⁻¹, mostly in one meal. Liu & Morton (1994) recorded a maximum consumption rate of 61% of its dry body weight $\cdot$ meal⁻¹ for the subtidal *N. siquijorensis*. Cheung (1994) obtained a similar value for *N. festivus* and showed that, energetically, such a meal could enable the animal to survive a further 21 days without further food, although starved scavengers, e.g. *Babylonia lutosa* and *Nassarius festivus* can, in fact, survive starvation for much longer than that, i.e. ~100 days (Morton 1990). It is clear, therefore, that the energetic advantage of scavenging is a real one.

Ilyanassa obsoleta feeds on carrion, but is described by Curtis & Hurd (1979) as an obligate omnivore, also feeding on algae and even predated the eggs and juveniles of *Cerithiidea californica* (Race 1982). When 50 adult *Ilyanassa obsoleta* were provided mussel tissue, *Geukensia demissa*, and allowed to feed to satiation without competition, the mean time spent on the food was 14.1 min. Size and the time spent feeding was poorly correlated over the range of sizes investigated. In contrast, when Curtis & Hurd (1979) maintained laboratory populations on three separate dietary regimes (shrimp, spinach and a mixture of both), they found that only snails maintained on the mixed diet exhibited growth during the 13 month experiment. *Ilyanassa obsoleta* is apparently unique among the Neogastropoda in that it possesses a crystalline style (Noguchi 1921, Jenner 1956, Brown 1969). Other nassariids are, however, known to harbour carbohydrase enzymes. *Nassarius reticulatus* produces high levels of laminarinase, although there is no record of this species feeding upon brown algae (Kristensen 1972). *Bullia digitalis* contains α -amylase, cellulase, laminarinase and cellulolytic symbiotic bacteria in the gut and ingests green algae growing on its shell (Harris et al. 1986).

Precisely how much food is required by a scavenger varies. McKillup & Butler (1983) have shown that the relative degree of hunger expressed by *Nassarius pauperatus* on several sandy shores in South Australia is a reflection of the availability of food to them in the field. Kideys & Hartnoll (1991) measured food consumption by *Buccinum undatum* and suggested that 27.5% of this intake is spent on pedal (locomotion) and hypobranchial (pallial cavity cleaning) mucus production. Absorption efficiencies were shown to be high (88%) for *Bullia digitalis* feeding upon mussel gill tissue (Stenton-Dozey & Brown 1988, Brown et al. 1989). High absorption efficiencies are advantageous for animals which rely upon unpredictable food supplies, such as carrion. Food consumption in proportion to body weight was found to be much greater in smaller individuals of *B. digitalis* than in larger (Stenton-Dozey & Brown 1988). The annual production of *Ilyanassa obsoleta* tissue on a Connecticut mudflat was estimated to be $20.0 \text{ g} \cdot \text{m}^{-2}$, of which less than 1% was contributed by juveniles (Edwards & Welsh 1982). From adult weight loss after spawning, it was estimated that 66%

of annual production was allocated to reproduction. Gross trophic efficiency calculations indicated that most consumption by *I. obsoleta* was not assimilated, but was defaecated. This is in striking contrast to the high assimilation efficiencies reported for *Bullia digitalis* (Stenton-Dozey & Brown 1988), but should be expected of an indiscriminate detritivore. Mucus production by *Ilyanassa obsoleta* was estimated to be 80% of total assimilation (Edwards & Welsh 1982).

Just as predatory snails consume more food during gametogenesis (Ansell 1982a, b), so do gastropod scavengers. Feeding activity in the north temperate whelk, *Buccinum undatum*, is maximal from late autumn to early spring and decreases sharply with the onset of breeding in late May (Martel et al. 1986). For lysianassid amphipods, Hargrave (1985) indicated that swimming and reproduction would necessitate greater energy intake. However, in the shallow-water lysianassid *Anonyx sarsi*, female meal size apparently decreases with increasing sexual maturity (Sainte-Marie 1987). We have already indicated that, on the basis of morphological and other criteria, deep-sea lysianassid amphipods comprise at least two feeding guilds: those which are adapted primarily for necrophagy and those which seem to rely on a more catholic diet (Dahl 1979). Similarly, on the basis of a study of the mandibles and guts of various shallow-water lysianassids, Sainte-Marie (1984) concluded that *A. sarsi*, with a capacious gut, is a "highly adapted" necrophage while other species, e.g. *Onisimus litoralis* and *Orchomenella pinguis*, were thought of as scavenging omnivores. *Anonyx sarsi* is able to survive up to 30 days of starvation, whereas *Onisimus litoralis* and *Orchomenella pinguis* were either dead or debilitated after being starved for between only 10–15 days, suggesting, again, that species of *Anonyx* are "obligate carnivores" (Sainte-Marie et al. 1989).

Human impacts

Fisheries

It is becoming increasingly important that we recognize the profound impact man imparts to the marine environment, its communities and biota (Underwood & Kennelly 1990). The fishing industry, for example, extracts >80 million tonnes (t) of fish products from the sea each year in what was once, but no longer, considered a wholly renewable resource. Marine fisheries impact scavengers in two ways: by (a) removing them from the sea and (b) by artificially promoting their success. The latter is usually a much greater impact than the former.

Apart from the numerous opportunistic scavenging crustaceans collected for human consumption, perhaps the best example of a scavenger fishery is that of whelks. In 1983, the French fishery for *Buccinum undatum* stood at 4000 tonnes·year⁻¹ with a commercial value of FF17 million (Santarelli & Gros 1984). Baited pots are laid on the sea bed and whelks are attracted to them from between 2.2–9.2 m in less than six hours (Sainte-Marie 1991). Catchability is, however, dependent upon many factors, notably site and season (Martel et al. 1986, McQuinn et al. 1988, Himmelman 1988). Other whelks are also the subjects of local fisheries, i.e. *Babylonia* off the coast of China (Morton 1990) and *Busycon* off Virginia, USA (Dicosimo & Dupaul 1985). The extent of both fisheries are difficult to assess. There are no statistics available for the *Babylonia* fishery but the species is

commonly encountered in fish markets along the Chinese coast. The *Busycon* fishery is a by-catch industry with *B. carica* harvested during crab dredging and *B. canaliculatum* harvested from surf-clam, crab-pot and flounder-trawl fisheries (Dicosimo & Dupaul 1985).

Human activities promote scavenger success by providing them with food resources that otherwise would be unavailable. In Norwegian and Arctic waters, lysianassid amphipods, especially *Anonyx* and *Tmetonyx*, scavenge and damage fish caught in nets and on long lines (Vader & Romppainen 1986). Conversely, trawlers dragging beam and otter trawls over the sea bed damage benthic shelf communities, providing regular supplies of carrion for scavengers. Morton (1994) has suggested that the local dominance of *Nassarius siquijorensis* in a subtidal habitat in Hong Kong may be attributed to local trawler damage of the epibenthos.

Trawling is a poorly focused fishery, i.e. more is captured than sought. The unintended component of each haul is known as by-catch. Andrew & Pepperell (1992) provide a thorough review of many aspects of trawl fisheries by-catch, but our major focus will be the impact of discarded carrion upon scavengers and scavenging.

The quantity of discarded by-catch varies considerably throughout the world, but usually exceeds greatly that of the targeted fishery. Only in countries where a fishery is either predominantly artisanal or consists of small vessels making daily landings is the by-catch quantity usually small. In this situation, a large proportion of the by-catch is used for either human or animal food with relatively little discarded (Grantham 1980). As fishing fleets become larger and increasingly mechanized, however, there is both a greater quantity and wastage of the by-catch. For example, for many decades, Indian fisheries discarded little (George et al. 1981) but as new, modern, vessels joined the fishing fleet, coupled with a relative decrease in available cold storage space, both the total quantity and proportion of discarded by-catch from Indian waters has increased (Gordon 1988, Sivasubramaniam 1990). Prawns, which contribute between 70–75% of the annual value of the trawl fishery of Karnataka, India, comprise only 13% of the annual average trawl catch (Sukumaran et al. 1982). Similarly, the weight of the by-catch by Australian trawlers in the Torres Strait is almost six times that of the prawns, the latter amounting to between 1000–1500 t·year⁻¹ (Somers et al. 1987, Channells et al. 1988). Andrew & Pepperell (1992) list 43 countries or regions in which the yield from trawling exceeds 5000 t·yr⁻¹. Most of these nations, such as the USA, Japan, Mexico and Australia, return most of the by-catch to the sea. The quantity of discarded by-catch is often unknown but, where estimates are available from the last decade, examples range from up to 1.83 million t for US fisheries (Gulland & Rothschild 1984), between 365 000 to 730 000 t for Mexico fisheries (Gulland & Rothschild 1984), and between 100 000 to 200 000 t for Australian fisheries (Harris & Poiner 1990). Estimates of Chinese, Japanese and most European fisheries discarded by-catch are either not available or unknown (Andrew & Pepperell 1992).

A high percentage of trawler by-catch consists of fin-fishes, but it also includes a variety of invertebrates, sea turtles, cartilaginous fishes and other fauna (Andrew & Pepperell 1992 and papers cited therein). Perhaps more germane to the present discussion, most of the by-catch consists of injured, dying or dead fauna. The few efforts to develop fisheries from mechanized prawn trawler by-catch have, more often than not, proved unsuccessful (Prabhu et al. 1978, Snell 1978, Barratt 1986). Thus, when returned to the sea, by-catch contributes a carrion windfall to marine scavengers (Maclean 1972, Seidel 1975, Saila 1983, Cushing 1984, Gulland & Rothschild 1984, Howell & Langan 1987).

Australian prawn trawlers in the Torres Strait contribute about 7000 t of by-catch carrion to the Coral Sea each year (Somers et al. 1987, Channells et al. 1988). Harris & Poiner

(1990) similarly estimated the total weight of the by-catch of Torres Strait prawn trawlers to be 6930t in 1985 and 4630t in 1986. Most comprised teleost fishes, i.e. 5520 and 2910t in 1985 and 1986, respectively. Ninety-nine percent of the by-catch was discarded. Of this, ~ 70% sank but an estimated 40% of the teleost catch (between 1200–2200t) floated. In contrast, Hill & Wassenberg (1990) showed that non-commercial crustaceans and cephalopods made up about 80% of the discards from prawn trawlers and most died, subsequently. The remaining 20% mainly comprised turtles, sharks, bivalves and sponges, most of which survived return to the sea. Sharks and dolphins fed on floating discards at night. Common and Black-crested terns, *Sterna hirundo* and *S. bergii*, and Greater frigate birds, *Fregata minor*, scavenged only during the day. Observations on baits set on the bottom showed that nemipterid teleosts and sharks ate most of the material; scavenging by invertebrates was negligible.

Moreton Bay prawn trawlers discard about 3000 tonnes each year (Wassenberg & Hill 1990). About 3% of this, mostly comprising fish, is floating carrion eaten by Silver gulls, *Larus novaehollandiae*, Crested terns, *Sterna bergii*, and, to a lesser extent, dolphins, *Tursiops truncatus*. Since fishing is at night, last discards are dumped around dawn when cormorants, *Phalacrocorax varius*, also begin feeding. Most trawler discards sink, including crustaceans (54%), echinoderms (18%) and a mixture of elasmobranchs and "rubble". About half the fish that sink are eaten by dolphins and diving birds. Some 11% of the discards that reach the bottom comprise fish and crustacean carrion that is eaten by crabs, e.g. *Portunus pelagicus*, and fish. Paul (1981) suggested that fish remains found in the portunid crab, *Callinectes arcuatus*, resulted from scavenging on dead fish discarded by fishermen. The remainder, chiefly crabs, echinoderms and elasmobranchs, reached the bottom alive. Thus, altogether, about 20% of all discards are eaten by surface and bottom scavengers. Wassenberg & Hill (1987) showed that *Portunus pelagicus* in Moreton Bay, Australia obtained ~ 33% of its food from the discards of prawn trawlers and that trawler by-catch may permit larger populations of the crab to exist than would otherwise occur. This is significant, because *P. pelagicus* is, itself, the subject of an important fishery (Thomson 1951), employing about 50 full-time fishermen (Williams 1980).

These and other studies (Andrew & Pepperell 1992) indicate clearly that trawling activity and its subsequently discarded by-catch transfers large quantities of biological material from the bottom to the surface and vice versa, making carrion available to both pelagic and epibenthic scavengers in quantities that would normally be inaccessible. Sheridan et al. (1984) developed a theoretical energy-flow model suggesting that a significant part of the discards from the Gulf of Mexico penaeid fishery was bacterially recycled, but the works just cited suggest a much more immediate recycling by scavenging. Globally, prawn trawlers discard an estimated 1.4 million tonnes of dredged material each year (Saila 1983). Clearly, the scavengers of the world's oceans have been receiving enormous carrion windfalls. The ecological impact of such amounts of carrion is unknown, but it is important that we begin to understand it. Increasing discards and changes in discarding practices may lead to false impressions not only of catch abundance but also of nutrient return to the sea. In coral-dominated areas such as the Torres Strait, the impacts of trawler discards may be profound.

Human fisheries resources impact bird populations. Many species follow fishing vessels where fish are being processed, e.g. Shetland Island trawlers attract Fulmars, *Fulmarus glacialis*, Great black-backed gulls, *Larus marinus*, Gannets, *Sula bassana*, and Great skuas, *Catharacta skua* (Hudson & Furness 1989). Great black-backed gulls and Gannets exploit the discards most efficiently, but some material such as gurnards and flatfish not taken by birds, eventually sink. The availability of discarded fish from trawlers has been

suggested as a cause of population increases in scavenging seabirds around the British Isles during this century (Hudson & Furness 1988), although the use by gulls of landfills (refuse tips) may also be important in this respect (Patton 1988). The latter author estimated that 90000 gulls foraged at seven landfills in Florida and that changing waste disposal practices from landfilling to incineration would likely affect them greatly. Notwithstanding, data on the breeding populations of gulls in southwest Wales collected over many years suggest that Herring gull and Great black-backed gull populations have decreased while populations of Lesser black-backed gulls have continued to increase at an approximately constant rate for 15 years (Sutcliffe 1986). Blaber & Wassenberg (1989) suggest that much of the food eaten by Pied cormorants, *Phalacrocorax varius*, Little pied cormorants, *P. melanoleucos*, and Crested terns, *Sterna bergii*, is derived from the discards of prawn trawlers in Moreton Bay, Australia. In fact, the population of ~350 *Phalacrocorax varius* possibly consumes 13.7% of the total fish by-catch. Moreton Bay trawlers produce about 7000kg of discarded by-catch each night. Although some of this is eaten by dolphins (Wassenberg & Hill 1990), most of the remainder is available to the birds and although there is no proof that seabird numbers have increased, this seems possible.

Furness (1982b) postulates that the numbers of several species of sea birds in the North Sea have increased markedly in response to increased availability of food caused by ecosystem changes induced by fishing: populations of Herring gulls, Skuas and Fulmars being dependent on discards from fishing boats, as in the Shetland Islands (Hudson & Furness 1989). Although British seabird populations have increased during this century (Cramp et al. 1974), such birds were hunted during the 18th and 19th centuries. Coulson (1963) and Potts (1969) believed that the increases were due to relaxation of such exploitation and that food supplies were and still are super-abundant. In contrast, Fisher (1952) argued that the dramatic increase in the Fulmar, *Fulmarus glacialis*, population in Britain and Ireland was caused by the rich new food supply made available by offal from whaling and whitefish trawlers. If overfishing can lead to a stock density reduction of 40% (Hempel 1978) and thus to reproductive failure, serious impacts on seabird population dynamics can be expected. It seems logical, therefore, that increases in the availability of floating fish in the discards of trawlers could have the opposite effect and, although such evidence is, at best, tenuous, the subject has been reviewed by Furness (1982a). The potential influence of discarded trawler by-catch upon seabird population structures is another variable which brings into question the use of seabird numbers as monitors of fishery prey stocks (Wilson 1992, Adams et al. 1992).

In the North Pacific, an estimated 170000km of gill net, 5500km of trawl net, 2000km of purse seine and 8900km of miscellaneous fishing gear are available for use by the major fisheries (Uchida 1985). Together, the North Pacific salmon and squid fisheries may set 21300km of driftnet each night. Estimates of the overall rate at which nets are lost is not available, but estimates for the US and other groundfish trawlers fishing in the southeast Bering Sea and Gulf of Alaska suggest that either all or large portions of between 35–65 nets were lost annually by between 300–325 trawlers (Lowe et al. 1985). Seals, in particular, are attracted to floating nets containing captured and dying fish (Fowler 1987) and become entangled themselves. Laist (1987) reviews the literature on lost net sightings and suggests that present levels of net debris in the North Pacific may be dangerously high, at least for fur seals. All such seals, fish, birds and numerous other animals trapped in lost netting must end up as marine carrion. Summer surveys of the incidental catch of marine birds and mammals in fishing nets around the east coast of Newfoundland indicated that over 100000 animals were killed in nets during a 4-year period (1981–84) (Piatt & Nettleship 1987).

Jones (1992) notes that the Japanese drift net fleet consists of 600 vessels; the fleet fishes for tuna and squid using drift nets up to 37 km in length and 15 m in depth. A 1990 study showed that in that year alone, the Japanese fleet killed 41 million non-target sea creatures, including 39 million other fish, 700 000 sharks, 270 000 sea birds, 26 000 cetaceans and 400 sea turtles (Jones 1992). Such corpses are mostly available as carrion to the remaining sea life.

Environmental perturbation and pollution

Environmental perturbations, including both disturbance of physical habitats and mass mortality of marine populations, have the potential to both increase carrion in the marine environment and enhance the number and diversity of scavengers. There is a vast literature supporting the hypothesis that moderate disturbance of the physical environment enhances local biological diversity, e.g. Dayton & Hessler (1972), Connell & Keough (1985), Sousa (1985) and Lake (1990). In some of these situations, scavengers are the beneficiaries. For example, several large marine animals are so highly disruptive to subtidal bottom environments that they damage many infauna and leave them vulnerable to wandering scavengers. Walrus excavate extensive subtidal flats in search of bivalve prey, exposing uneaten, damaged, bivalves to a variety of scavengers including the asteroid *Asterias amurensis* and the ophiuroid *Amphirodia craterodonta* (Oliver et al. 1985). Gray whales excavate large (2–20 m²) areas of the sea floor originally stabilized by dense tube mats constructed by ampeliscid and other amphipods. Large numbers of lysianassid amphipods, especially *Anonyx* spp., occupy these craters rapidly and attack injured and dislodged polychaetes, small crustaceans and other invertebrates. Within hours of the initial feeding disturbance by Gray whales, the cratered sea floor contained 20–30 times the numbers of lysianassid amphipods than the surrounding tube mats (Oliver & Slattery 1985). Feeding shore birds on a tidal flat can produce similar, albeit smaller, disturbances. On Dutch shores, the Black-headed gull, *Larus ridibundus*, and the Shelduck, *Tadorna tadorna*, make characteristic feeding traces, the former digging trenches up to 3 m in length and the latter producing craters up to 60 cm in diameter (Cadée 1990).

Mass mortality is an environmental perturbation of biological populations. A variety of factors contribute to mass mortality of marine biota and include: (a) physical disturbance of habitats; (b) environmental variables such as temperature, oxygen or salinity reaching lethal limits; (c) disease; (d) natural toxins such as those produced by dinoflagellates during red tides and (e) man-made toxic pollutants. Mass mortality in the sea usually increases the amount of carrion (mortality either caused or followed immediately by burial is an obvious exception), but either may or may not be beneficial to scavengers. Broadly-focused causes of mass mortality, such as environmental variables which exceed survival limits, are likely to produce mortality among both scavengers and non-scavengers, as occurred at Rottnest Island, Australia during the summer of January 1991, when numerous species of reef invertebrates, including scavengers, succumbed to excessively high air temperatures coinciding with low spring tides. Any scavenging individuals which survived the perturbation, such as some of the opportunistic *Thais orbita*, fed upon the carrion windfall (Morton & Britton 1993). More narrowly focused causes of mass mortality, such as disease impacting either one or a few related species, e.g. Caribbean populations of the sea urchin *Diadema antillarum*, discussed earlier, and the distemper virus which decimated phocid seals in European coastal waters in 1988 (Moutou et al. 1989), may produce an instantaneous carrion windfall available to all scavengers capable of exploiting it.

Mortality associated with dinoflagellate red tides include both direct toxin poisoning (Riley et al. 1989, Toyoshima et al. 1989, O'Shea et al. 1991) and secondary anoxia (Yamaguchi et al. 1981, Ochi 1989, Lam & Yip 1990). Toxins accumulated in some biological tissues are transferred to higher levels of the food chain. In 1982, the death of numerous fishes, Double-crested cormorants, *Phalacrocorax auritus*, and 37 manatees, *Trichechus manatus latirostris*, in southwestern Florida was attributed to potent neurotoxins (brevetoxins) produced during a widespread bloom of the dinoflagellate, *Ptychodiscus brevis* (= *Gymnodinium breve*) (O'Shea et al. 1991). Just as some filter-feeding zooplankton (White 1981, Hayashi et al. 1982) and bivalves are immune to these toxins and are, hence, capable of passing them on to higher levels of the food chain, invertebrate scavengers may also be immune to toxins contained in carrion tissues killed by them. Not all bivalves are unaffected by red tides. Bay scallops, *Argopecten irradians concentricus*, not previously exposed to a *Ptychodiscus brevis* red tide, suffered significant recruitment failure in 1987 during the first recorded outbreak of this dinoflagellate in North Carolina (Summerson & Peterson 1990). Although oysters often survive red tides when they ingest and concentrate sufficient numbers of dinoflagellates to discolour their digestive tissues brick-red (Hata et al. 1982), mass mortalities of oysters and other shellfish either during or following a red tide is often the result of anoxic water (Cho 1979). Fish kills in the North Sea are frequently attributed to anoxic water conditions associated with either eutrophication or plankton blooms or both (Gerlach 1984).

Mass mortality, regardless of cause, may generate large quantities of carrion in the marine environment, but it is available to scavengers for only a short time. Even recurring mass mortality events, e.g. red tides, usually occur again after a long, often unpredictable, quiescence (Marasovic 1989, Usup et al. 1989, Kondo et al. 1990, Thomas & Gibson 1990). Such ephemeral, unpredictable, infusions of carrion, although a temporary windfall, seem inadequate to sustain a feeding strategy exclusively dependent upon it. Thus, facultative rather than obligatory scavenging behaviour seems to have a selective advantage for any species capable of feeding on carrion.

The environmental perturbations discussed so far are mostly natural events (Zijlstra & de Wolf 1988). Some, such as red tides, can be enhanced and accelerated by human activities, but have and will continue to occur without our interference. Unfortunately, human-induced perturbations are increasingly influencing marine communities and ecosystems.

There is little question that human-engendered activities have increased greatly the quantity of marine carrion. Trawling fisheries, as discussed above, are an environmental perturbation of the shallow sea bed. Even if all by-catch were retained by the trawler, the effects of drag lines on the bottom must be similar to that just described for feeding Walruses and/or Gray whales but of significantly greater magnitude. Many other human activities result in increasing mortality of marine species (Hartwig et al. 1985). Often seemingly benign man-made objects discarded in the sea are deadly to marine species (Laist 1987). Plastic six-pack beverage rings ensnare fishes, interfering with swimming, feeding and growth and may, eventually, result in death (Parker 1990). Plastic particles were found to be common pollutants in the stomachs of Wilson's storm petrels, *Oceanites oceanicus*, and Cape petrels, *Daption capense*, breeding in Antarctica (Franeker & Bell 1988). These particles were obtained apparently from wintering areas outside the Antarctic. Adult Wilson's storm petrels transferred plastic particles to chicks, many of which died before fledging. Fulmars, *Fulmarus glacialis*, from colonies on the Firths of Forth and Clyde, Scotland, commonly scavenge rubber contraceptives and sheet polythene from the sea surface during the day (Zonfrillo 1985). With the mean density of plastic particles in the

sea now estimated to be between 1000 to $400 \cdot \text{km}^{-2}$, plastics have become a significant menace to many species of seabirds, especially members of the Procellariiformes (Azzarello & Van Vleet 1987). Members of this order, with small gizzards and an inability to regurgitate ingested plastics, are at highest risk. Planktivores have a higher incidence of ingested plastics than piscivores as the former are more likely to confuse plastic pellets with zooplankton. Also at risk are sea turtles which have a propensity to ingest plastic scraps and become entangled in lines and discarded netting (Carr 1987). Biofouling communities can accumulate on floating plastic objects, causing them to sink, but rapid defouling at depth may permit these objects to reappear at the surface several times, magnifying the hazards of plastics to sea birds, turtles and other susceptible fauna (Ye & Andrady 1991).

Oil spills are probably the most widely publicized form of pollution which bring mass destruction to marine life. Birds (Barrett 1979, Stowe & Underwood 1984), coastal marine mammals (Siniff et al. 1982, Engelhardt 1987, Williams et al. 1988, Ralls et al. 1992) and intertidal invertebrates (Vandermeulen 1982) are especially vulnerable. Even some dispersants used to treat oil-contaminated environments have proved to be highly toxic to fishes and bivalves (Belkhir & Hadj Ali Salem 1986).

Since pollution, particularly organic enrichment, may either debilitate or kill affected marine organisms, it seems at least possible that such disturbed habitats may be occupied by more opportunistic species, possibly scavengers. There is, however, little direct evidence in support of this idea. Poore & Kudenov (1978) studied the benthos around an outfall of the Werribee sewage-treatment farm in Port Phillip Bay, Australia, and reported that the station closest to the outfall, i.e. within 300m, had "high proportions of scavengers and deposit feeders". Following a mass mortality of a demersal fish population in Kiel Fjord, Germany, due to anoxia caused by eutrophication, Prein (1988) recorded the mass occurrence of the free-living marine nematode *Pontonema vulgare* on dead fish, jellyfish, starfish and weakened mussels. Lorenzen et al. (1987) described a similar mass occurrence in the summer in the inner Flensburg and Kiel fjords with the nematode marking sharply the transition zone between aerobic and anoxic sites, the latter thought to have been the result of pollution.

Marine scavengers are not immune from pollution effects. The scavenging mud snail, *Ilyanassa obsoleta*, is especially susceptible to imposex, the development of male sexual characteristics in females (Jenner 1979), when exposed to tributyltin (TBT), a compound used in antifouling paints (Smith 1981, Bryan et al. 1989).

The epibenthic fauna of the Wadden Sea was surveyed during the years 1923–26 (Hagmeier & Käendler 1927). The study area was resurveyed in 1980 by Riesen & Reise (1982). These authors showed that, in the intervening years, substantial degradation of the benthic marine communities had taken place, largely the result, they suggested, of human interference. Natural oyster beds were overexploited, driving the local population of *Ostrea edulis* to extinction. An epidemic disease eliminated a *Zostera marina* bed in 1934 and it never became re-established. Reefs of the colonial polychaete *Sabellaria spinulosa* were destroyed by shrimp trawlers. However, large epibenthic predators and scavengers, i.e. crabs, snails and starfish survived all of the changes. Recently, Morton (1994) has suggested that the demise of specialist neogastropod predators from the polluted sea bed of Hong Kong (Taylor & Shin 1990) can be correlated with the enhanced success of scavengers, notably the gastropods *Nassarius siquijorensis*, *Philine orientalis* and species of *Babylonia* and some asteroids, e.g. *Luidia longispina* (Emson et al. 1992). Such species, physiologically able to tolerate eutrophication-induced near-anoxia of the sea bed, survive by feeding on the carrion engendered by both pollution and trawling.

Discussion

After surveying the groups that contain scavenging members and considering the environments where scavenging occurs, we finally come to conclude that scavenging behaviour is typically coupled with one or more additional feeding strategies. That carrion is a good, nutritious, food there can be no doubt. It has many advantages over both detritus and prey. Minimal effort has to be spent collecting it and handling it to gain entry, as would be the case with prey. There are, however, a number of problems with carrion: its availability is largely unpredictable both spatially and temporally and it is palatable only for a short time before bacterial decomposition renders it inedible for most macrophagous scavengers.

Are there, therefore, species of marine animals that feed exclusively upon carrion, or are marine scavengers only opportunists, supplementing their diets with carrion when it is available? Macrophagous scavenging seems to supplement the diets of many marine animals, including turbellarians, nemerteans, nematodes, polychaetes, many anthropods, echinoderms and fishes. Moribund tissue is not, however, their primary source of food. Even the hagfishes, renowned for their scavenging activities, are not restricted exclusively to a diet of carrion. If there are obligate scavengers among marine animals, they will most likely be found among the Crustacea and the Gastropoda. We will consider some general attributes of representatives of these two groups that come closest to our notion of what an obligate scavenger might be.

Obligate scavengers are unlikely to be found among most of the marine arthropods, given the wide range of food consumed by many species. Necrophagous arthropods are primarily carnivores, omnivores, detritivores or any combination of these. Arthropods may have specialized in many ways, but most shallow-water species remain adaptable with regard to diet. Too little is known with respect to the deep-sea crustacean scavengers to justify proclaiming any as definitive obligate scavengers, although the deep-sea representatives of the Lysianassidae (Amphipoda) come close to our concept of such an animal in that they are capable of withstanding long periods of starvation; demonstrate a relatively rapid response to a carrion-fall; locate the carrion efficiently; maximize the rate and amount of food consumed and utilize such food efficiently (Smith & Baldwin 1982). There is not, however, unequivocal evidence that any lysianassid is exclusively necrophagous.

Although representatives of the Nassariidae occur mainly on soft sediments at all depths of the sea (Cernohorsky 1984), they are most obvious and best studied on the shore. Dietary preferences of intertidal nassariids are poorly focused, and several species rely upon either detritus or primary producers for sustenance in addition to carrion (Britton & Morton 1993a). The supply of carrion to beaches throughout the world is unpredictable. It is sometimes possible that more washes ashore than intertidal scavengers can process. At other times, the beach may remain free of carrion for extended periods of time. To counter this, nassariids and buccinids are able to survive prolonged periods of starvation. Laboratory-held specimens of *Nassarius festivus* and *Babylonia lutosa* both survived > 100 days without food (Morton 1990). *Nassarius obsoletus* similarly can survive up to 120 days without food (Curtis & Hurd 1979). Cheung (1994) calculates that a single meal will sustain respiration in *N. festivus* for periods of > 20 days. With such an unreliable food source, intertidal scavengers may also seek alternative foods that can sustain them through carrion-deficient times. Some species, such as *Ilyanassa obsoleta*, opportunistically consume what carrion washes in, but seem capable of living many months on detritus and algae. Others, such as *Bullia digitalis*, represent the opposite extreme. This species seemed to be the best candidate for an obligate scavenger, but this is not so. A. C. Brown had studied *B. digitalis* intensely

for 25 years before it was discovered that this nassariid, like several other members of the family, could feed and possibly sustain itself upon algae which grow on its shell (Harris et al. 1986). *B. digitalis* and *Ilyanassa obsoleta* are also now known to eat live prey (Brown et al. 1989, Race 1982). Upon closer examination, it is likely that most Nassariidae rely upon a variety of alternate food sources in the absence of carrion. Although the diets of subtidal nassariids are virtually unknown (the diets of over 80% of the family are unknown), it is equally unlikely, given the constraints imposed by their environment, that obligate scavengers will be found amongst them.

Marine scavengers are, thus, most likely exactly what they seem – opportunistic omnivores capable of deriving nutrition from a variety of sources. Intertidal scavengers may be able to locate carrion more efficiently than their subtidal counterparts, but this seems more a function of environmental fostering than organismal specialization. The surf-entrained *Bullia digitalis* is possibly a notable exception and the Lysianassidae and the Nassariidae, as lineages, may represent the closest attempts at an obligate scavenging life style. Representatives of both occasionally (or frequently) must seek food sources other than carrion for survival. It remains to be determined how the Nassariidae, seemingly within the mainstream of neogastropod evolution with respect to most attributes, have deviated so markedly with regard to the variety of foods utilized, and the surprising opportunism of at least some species which have possibly reverted to herbivory, as in the case of *Ilyanassa obsoleta* with an intestinal crystalline style (Brown 1969). The general lack of obligate scavenging in the sea emphasizes the importance of a sustainable source of food in the evolution of specialist feeding strategies and, conversely, the importance of carrion to a wide variety of dietary generalists which exploit it opportunistically.

We do not doubt that the terrestrial ecosystem has favoured the evolution of obligate scavengers and that these may venture onto the shore occasionally, e.g. vultures and carrion flies. We similarly do not doubt that many shore-dwelling animals may revert to scavenging opportunistically, as we have demonstrated for numerous birds, arthropods and even gastropods. We do, however, have problems with the notion of obligate scavenging in the sea, for a variety of reasons. First, what we see today and in recorded history, is the product of our time. Morton (1994) has suggested that the high incidence of scavenging nassariids on Hong Kong's shores and subtidal habitats results from perturbation, i.e. environmentally damaging fishing techniques and pollution. Thus, on a polluted beach, Starfish Bay (Hoi Sing Wan), nassariids, *Nassarius festivus*, occurred at frequencies of $<4 \cdot \text{m}^{-2}$ in 1973; today their numbers exceed $60 \cdot \text{m}^{-2}$, suggesting artificial population enhancement. Subtidal scavenging snails, notably *N. siquijorensis*, also outnumber any predator. The high numbers of sea birds in the British Isles during the 1960s and 1970s have been attributed to the ready availability of carrion from fishing boats (Furness 1982b) and from "open" landfill sites (Greig et al. 1985, 1986, Monaghan et al. 1986). Sanitary landfill sites and fish processing on land may have reduced carrion availability, resulting in a decline in flock numbers. Today, many sea birds numbers are suffering a decline in Europe (Anonymous 1989).

The analyses of Moreton Bay and Torres Strait prawn trawler discards and their ultimate fate is also revealing (Somers et al. 1987, Channells et al. 1988, Wassenberg & Hill 1990). That which floats, i.e. mostly fish, is consumed by birds, fish and cetaceans; that which sinks is similarly eaten by fish and crustaceans with, presumably, smaller invertebrates picking up the final pieces. Slavin (1982) estimated that, world wide, between 3–5 million tonnes of by-catch is discarded by shrimp trawlers each year. Such material must be having a profound influence on any marine animal that is capable of scavenging, regardless of what other feeding methodologies it might otherwise typically either utilize or favour. This may,

in turn, inflate the true significance of marine necrophagy as perceived by humans. Just as sea-floor disturbances by Gray whales and Walruses enhance the local environment for scavengers (Oliver & Slattery 1985, Oliver et al. 1985), so trawling and/or dredging, by damaging many inhabitants of the sea bed directly, enhances the survival of scavengers such as nassariids and lysianassids, the former protected from significant damage by small size and thick shell, the latter migrating into the area after the damage is done, and both surviving to reap the nutritive rewards. Studies of shoreline litter (Ross et al. 1991) show, as do previous studies, that most of this is generated as rubbish on land and that what we typically see, i.e. plastics, paper, wood, rubber, glass, styrofoam and metal, is probably only a small reflection of what is put in the sea as edible material from various sources.

Even in the deep sea, human impacts are felt. Davies (1987) reported that the contents of a 3 m Agassiz trawl from a depth of 3000 m yielded ~ 5000 items of human origin compared to 560 animals retained by the same net. Items caught ranged from plasterboard, a shoe, bottles, clothing, plastic, polythene, coat hangers, laminated board and tin and aluminum cans. Presuming that all this is dumped from ships, how much food, potentially available to scavengers is also thrown overboard and, after sinking, supplies deep-sea opportunists as well?

It is, however, also a sobering thought that were it not for marine necrophagous scavengers, the "carriion" that man either puts into or creates in the sea would undergo saprophytic degradation with, possibly, more severe consequences. Just, therefore, as vultures and carrion flies keep the terrestrial domain free of rotting corpses, so do a variety of marine opportunists.

We, thus, conclude that the spatially and temporally infrequent occurrence of natural carrion in the marine environment has not favoured the selection of obligate scavengers. Notwithstanding, representatives of many taxonomic groups will scavenge opportunistically to supplement normal diets. Typically, the feeding strategies of predators are best suited to exploit such nutrient windfalls, with lysianassid crustaceans and nassariid gastropods being the best examples of such animals.

We are concerned, however, that human activity in the sea, especially fishing and pollution, has promoted the artificial "success" of species which can opportunistically exploit such perturbations. The impact of fisheries in promoting the success of scavengers is better documented than that of pollution. The massive accumulation of human-generated carrion in the sea, either by the discarding of by-catch, wanton destruction of non-target species in nets or by pollution-induced mortality, not only has the potential to alter community structure profoundly in several marine environments, but there is already evidence that it has occurred. Humans have successfully spread a few "trash" species, e.g. cockroaches and rats, across continents and now, it seems, we are, either knowingly or unknowingly, intent on promoting more opportunists in the sea. In a review of marine mollusc introductions into North America during the 19th and 20th centuries, Carlton (1992) has shown that *N. fraterculus* has been introduced into bays of the Northeast Pacific from the Northwest Pacific, as have *Busycotypus canaliculatus* (Melongenidae) and *Ilyanassa obsoleta* (Nassariidae) from the Northwest Atlantic. Carlton (1992, p. 492) notes, for example, that *I. obsoleta* is "astronomically abundant in San Francisco Bay". In some locations, it has replaced the native mud snail, *Cerithidea californica*, by competitive interactions and egg capsule predation (Race 1982). The significance of this well-known scavenger in the introduced part of its range is, however, unknown and it seems to us, in conclusion, that the rôle and significance of marine scavengers has been largely ignored for too long.

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